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BIOLOGY

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A REVISION OF CEDRELA
(MELIACEAE)

C. EARLE SMITH, JR.

FIELDIANA: BOTANY
VOLUME 29, NUMBER 5

Published by
CHICAGO NATURAL HISTORY MUSEUM
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BIOLOGY

INTERIOR OF OLD CATHEDRAL AT COMAYAGUA, HONDURAS

Apparently all of the wood visible in the photograph is Spanish cedar (*cedro*), including that of the altar, which is overlain with gold leaf. This clearly points up the endurance of *cedro* as well as the ease with which it may be worked. Photograph by Louis O. Williams.

A REVISION OF CEDRELA
(MELIACEAE)

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Biology

A Revision of Cedrela (Meliaceae)

Cedrela (Meliaceae) is a genus of trees of the American tropics and subtropics. A number of Old World species have, at times, been included in the genus, but these belong to the genus *Toona*. I shall treat only the American species in detail, although the African and Australasian species have been examined.

The family Meliaceae is a large natural group of woody plants which are largely restricted to the tropics and the subtropics. A few are hardy well up into temperate climates. Within the family, foliage varies from simple to pinnately compound, and the inflorescences are usually racemose, although the lower branches may be so elongated in relation to the upper branches as to form a cymose panicle. The fruit may be a drupe or a berry, but most of the genera have capsular fruit. Flowers exhibit many combinations of free or united parts; basically, they are pentamerous.

Cedrela is a clearly defined genus in the American tropics. Both *Guarea* and *Trichilia* include a number of American species, none of which can be confused with species of *Cedrela* because of their staminal tube and three-valved fruit with wingless seed. Similarly, the smaller genera, *Carapa, Cabralea* and *Odotandra,* are clearly separated from *Cedrela* by characters like those of *Trichilia* and *Guarea.* Only *Elutheria* and *Swietenia* have winged seed dispersed from a five-valved capsule; the former genus has the valves of the capsule dehiscing from the apex but held by a network of fibers at their margins; *Swietenia* capsules open from the base and the wing of the seed forms between the seed itself and the point of attachment to the placenta. *Cedrela* capsules open cleanly from the apex; the seeds are attached firmly to the placental tissue and the wing forms on the opposite side of the seed. Both *Elutheria* and *Swietenia* have staminal tubes, but the stamens of *Cedrela* are free except for their adnation to the gynophore. On the basis of wood anatomy, though, Kribs (1930) indicates that *Cedrela* is more closely related to *Swietenia* and *Carapa* than to other genera in the family.

During the past few years, the confusion surrounding the nomenclature of specific taxa in *Cedrela* has been emphasized by the increas-

ing use of Spanish cedar (*cedro*) as a reforestation subject. Both in the American tropics, where it has been widely planted as an ornamental tree and a shade tree for coffee plantations, and in the tropics of the Old World, foresters have experimented with *Cedrela* because of its quick growth, clean bole, and relative freedom from diseases. The lumber has always been in demand in Latin America. Most of the distribution of *Cedrela* for reforestation has been accomplished by seed from trees growing at or near botanical and forestry establishments. Almost invariably the name *Cedrela mexicana* has been applied to these stocks of seedlings, while the epithet *C. odorata* has been considered to apply only to West Indian *cedro* trees (which seldom seem to have been used as a source). Actually, *C. mexicana* and *C. odorata* are the same species, and seed lots of another species of wide distribution in Latin America (*C. angustifolia*) have been used by the foresters. While little can now be done to unravel the past confusion in forestry literature, this study will serve to reduce the confusion among foresters concerning their current field material.

Acknowledgments

I wish to extend my heartfelt thanks to my many friends in tropical American botany who have blessed this project verbally while wisely and sadly shaking their heads. Perhaps I shall need their sympathy even more, now that I have done such mayhem.

The American Philosophical Society most generously awarded me grant No. 167 from the Johnson Fund, which made possible a trip to southern Mexico, Panama and Venezuela to study *Cedrela* in the field. An earlier trip with a group of foresters provided valuable knowledge of the practices used in establishing plantations of *Cedrela* in the West Indies and Central America.

I sincerely appreciate the help extended by Dr. Eizi Matuda of the Instituto Biologico in Mexico City. Prof. Efraim Hernandez X. was exceptionally helpful in arranging transportation and the assistance of a student, Sr. Frederico Ruiz Mora. Mr. Thomas MacDougall offered freely his time in the field and much information about the Tehuantepec area, which he knows intimately.

Mr. H. Morgan Smith of Canal Zone, Panama, generously provided accommodations, transportation and assistance. Sr. Gertrudis Arauz of Gatoncillo, Panama, was most helpful in the field.

In Venezuela, I found perfect hospitality in the home of Dr. Tobias Lasser, who also made available to me the facilities of the Instituto Botánico in Caracas. Dr. Leandro Aristeguieta and Sr. Ernesto

Foldats of the Instituto provided generously of their time and hospitality. The staff of the Instituto Forestal made me more than welcome in Merida. Dr. Richard Jorgensen accompanied me to the Paramo de la Negra. Dr. J. P. Veillon, Dr. Hans Lamprecht, and others of the Instituto arranged for an assistant and transportation and also provided a complete set of photographs of *Cedrela* specimens taken by Dr. Luciano Bernardi in numerous herbaria of Europe and North America.

I wish to extend especial thanks to Dra. Maria Buchinger of Argentina, who furnished information about *C. tubiflora* Bertoni.

I am indebted to Dr. Howard Arnott of Northwestern University, who cleared and stained leaflets of all of the species of *Cedrela* for anatomical study.

The following herbaria provided the bulk of the exsiccatae which I have examined; the abbreviations are those suggested by Lanjouw and Stafleu (Index Herbariorum):

A	Arnold Arboretum, Cambridge, Mass.
F	Chicago Natural History Museum
GH	Gray Herbarium, Cambridge, Mass.
MO	Missouri Botanical Garden, St. Louis
NY	New York Botanical Garden
PH	Academy of Natural Sciences, Philadelphia
US	United States National Herbarium

I am especially grateful to the curators of the following herbaria, who responded to an emergency appeal for obscure entities:

B	Botanisches Museum, Berlin–Dahlem
LE	Komarov Botanical Institute of the Academy of Sciences, Leningrad
S	Naturhistoriska Riksmuseum, Stockholm

History

Spanish cedar has been used extensively for lumber since prehistoric times in tropical America. The Spanish explorers used the name *cedro* because of the aromatic odor of the wood, which they associated with the true cedars of the Old World. The earliest literature refers to the genus as *Cedrus*, a generic name which appears as late as 1759 in Phillip Miller's *The Gardner's Dictionary* (ed. 7).

Cedrela was established as a generic name by Patrick Browne in 1756 in his *Civil and Natural History of Jamaica*. Plate 10 in that publication is unmistakable; it includes details of the fruit, flower and seed. Browne's comments are further evidence for the identity of the plant which he had: " . . . . The trunk is covered with a rough bark marked with longitudinal fissures, which as well as the berries and

leaves, has so disagreeable a smell while fresh, that few people care to go into the woods where any of those trees have been recently cut down; the timber, however, has a pleasant smell; it is very full of a dark resinous substance, light, porous, and easily worked; . . . ." Linnaeus published the species *C. odorata* in 1759 (Syst. Nat. ed. 10:490), citing the Browne plate, so that this stands as the type of the genus and the species. The specimens in the Linnaean herbarium are not to be considered as type material. No. 274.1 is not *C. odorata* and is so annotated by J. E. Smith. While the leaf of No. 274.2 may be referable to *C. odorata,* foliage is so markedly variable in *Cedrela* that identification of this leaf can never be certain. Furthermore, there is no reference on either specimen to indicate that it had been received before the publication of the specific epithet.

In 1830, Adrien de Jussieu published *Mémoire sur le groupe des Méliacées,* providing a detailed description of the morphology and anatomy of many members of the family Meliaceae. His taxonomic treatment presented only *Cedrela sinensis* and *C. guianensis.* Heretofore the meliaceous genera had been variously placed in the Myrtilles (B. de Jussieu, 1759), Pistachiers (Adanson, 1763) or Cedrelaceae (Robert Brown, 1814). A. L. de Jussieu had named the family Meliaceae in 1789. P. De Candolle (1824) divided the family into the tribes Melieae, Trichileae and Cedrelieae. Adrien de Jussieu again elevated the Cedrelaceae to family status with two tribes, Swietenieae and Cedreleae.

There were no further attempts to monograph the family Meliaceae or the genus *Cedrela* until 1878, when Casimir De Candolle treated the family in the first volume of the *Monographiae Phanerogamarum.* Earlier in the same year, the section on the Meliaceae in Martius' *Flora Brasiliensis* had been published under the authorship of De Candolle, who followed the treatments of earlier authors and added two species and four varieties. Roemer (1846) had made the division between *Cedrela* (for the New World species) and *Toona* (for the Old World species), but De Candolle chose to keep the Asiatic species in *Cedrela.*

Numerous species and varieties were added to *Cedrela* over the years without another critical revision of the genus. Harms (1896) separated *Cedrela* and *Toona* again in his article in *Die Naturlichen Pflanzenfamilien.* C. De Candolle (1908) pulled them back together. In his summary of the family, Harms (1896) elevated the tribes of De Candolle to subfamily position and erected beneath them a new tribal grouping with subtribes in which the subfamily Cedreloideae

contains one tribe, Cedreloideae, and two subtribes, Cedreleae and Ptaeroxyleae. In his later treatment, Harms (1940) added the subtribe Cedrelopsideae.

Otto Kuntze (1891) created a mass of synonyms in *Cedrela* as he did in many other genera. Following his convictions on priority, he chose Rumphius' genus *Surenus* (1743) as the repository for *Cedrela* species names. Under the instructions for citing name-bringing basonyms (Article 32, International Code of Botanical Nomenclature, 1956), only *Surenus Brownii* (Loefl.) O. Ktze. qualifies as a legitimate transfer. But even this is a mistaken interpretation of the Loefling work from which it was cited (see discussion under *C. odorata* L.). Thus, I am citing only this Kuntze combination in the synonymy of *Cedrela*, preferring to let the remainder rest undisturbed so as to reduce the lists of synonymy.

By 1954, there were 37 validly published *Cedrela* species names applied to American trees listed in *Index Kewensis*, with a number of varieties and forms in the literature. None of the keys were practical because of the overlapping characters to be found in the plants. Almost any specimen could be placed in three or four species with little difficulty. Both field observations and a check of herbarium material led to the conclusion that the foresters would not be able to name correctly the stock with which they were working until a revision had been made.

After carefully examining the collections of *Cedrela* of both the Old and the New Worlds in several large herbaria in the United States, I came to two conclusions: (1) Roemer was indeed correct in dividing the Old and New World species, and (2) there is not enough herbarium material of the Old World species in the United States to prepare a critical revision of the genus *Toona*. The first decision is based upon the close relationship of all of the American species of *Cedrela* to one another and the distinct differences between this group of species and all of the species of *Toona*. All of the material of the latter genus which I was able to examine indicates that this is a very closely related group of species also.

A number of fundamental morphological differences separate *Cedrela* and *Toona*. Among the most important of these is the column forming the gynophore in *Cedrela* and its lack in *Toona*. In *Cedrela* the filaments are adnate to the surface of the gynophore. In *Toona* the expanded filaments form a pillow-like mass in which the ovary is generally partially buried (fig. 8). The petals of *Cedrela* are adnate to the gynophore through a carina on their inner surface. The flowers of the species of *Toona* which I have examined have the petal attached

by its very base to the top of the pedicel far beneath the mass of expanded filament tissue. The calyx in *Toona* is formed of five distinct lobes joined only briefly at the base so that the calyx opens flat or reflexes at anthesis. As the petals are joined only to the top of the pedicel, they, too, open widely. In *Cedrela*, the calyx segments are fused into a cup-shaped form; the adnation of the petals to the

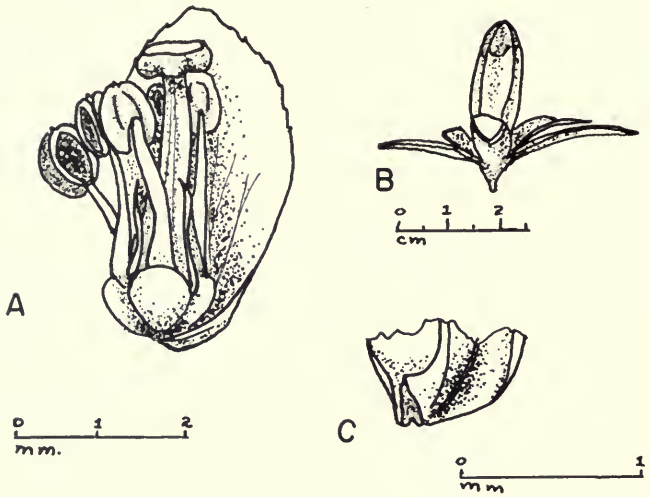


FIG. 8. Morphology of flower of *Toona*. A, Dissected flower of *Toona serrata* (Royle) Roem. showing petal inserted beneath mass of expanded filaments and staminodia alternating with stamens. The ovary base is surrounded by the pillow-shaped tissue formerly described as a disc. B, Fruit of *Toona sinensis* A. Juss. C, Base of a petal showing small area of attachment.

gynophore prevents their spreading outward except above the point of attachment. The fruits of the two genera are basically similar, the differences being mainly in degree of development, as the column in the fruit of *Toona* is merely angled, not winged, nor is there a distinct sterile apical area as in the fruit of *Cedrela*.

Because many of the species of *Toona* have staminodia alternating with their stamens, and because of formation of the mass of tissue surrounding the ovary, I believe that the androecium here is derived from a staminal tube of ten stamens which has become modified into its present form. *Cedrela* is clearly distinct from the other morphologically similar genera in the Meliaceae because of the five free stamens adnate to the gynophore only for a portion of their length. All of the necessary nomenclatural transfers into *Toona* have apparently been made by Harms (1940).

Economic Importance

From the earliest days of exploration and colonization in tropical America, Spanish cedar has been one of the most important timber trees of the area. It is frequently mentioned in early accounts. The first explorers undoubtedly learned of its value from the natives of the area, who still use it extensively for canoes and house timbers.

Browne (1756) has an interesting implication in the first sentence of his description of the uses of "Barbadoes Cedar"—"This tree *was* very common, and *still* continues to grow in many parts of the island" (the italics are mine)—indicating that the exploitation of accessible stands of native forest was rapidly going forward in 1750. He notes that it was then used for structural timbers, finish lumber, cabinet work, and for canoes and *petiagers* (small boats), but that the lumber "cannot be made into casks as all spirituous liquors dissolve a great quantity of its natural resin and acquire a strong bitter taste from thence."

The wood of *Cedrela* became an article for the export trade during the 1800's when the cigar industry demanded the use of Spanish cedar for packing cigars. These fragrant boxes were commonplace before rising costs in the 1930's finally forced the cigar industry in the United States to turn to cardboard or less expensive wooden containers manufactured from soft native lumber (and frequently overprinted on the outer surface with a *Cedrela* grain pattern).

Cedro is still one of the most valued of the trees cut for local use throughout tropical America. It is soft and easily worked but is strong for its weight. The fragrant oil in the wood is a deterrent to insect attack, so that the wood is generally used in the construction of wardrobes and other household furniture. This property and its ease of handling make it a popular structural timber for building. Wherever it is used, the darker, harder heartwood of trees growing on drier sites is preferred. When grown with abundant moisture, the wood is lighter in color, less dense, and has a lesser oil content. I was told by the native craftsmen that they can distinguish the lumber from different species of *Cedrela*. In view of the statements in Record and Hess (1943) that the wood samples of different *Cedrela* species exhibit the same qualities under test and show the same structure, I suspect that the named kinds of *cedro* of the native craftsmen are merely variations in density and color of wood due to the influence of environmental factors during the growth of the trees. The woodsmen who cut *cedro* distinguish both the different species and the variations in

growth form within a single species (Acosta Solis, 1939, and personal observation).

Details on the total amount of *Cedrela* timber harvested each year are difficult to obtain, as much of the cutting is still carried on as a one-man business. The cutter may then sell his trimmed logs to a mill for processing, or he may hand-saw boards for local sale. There are occasional large-scale cutting and milling operations which flourish so long as there is cuttable timber on the owned or leased land which is being clear-cut, but these are not common. Large timber operation in Latin America is largely restricted to rivers, coastal areas or transportation routes accessible to salt-water transportation. The product of these mills is largely for export. Recently, there has been an increase in heavy harvesting to supply the few plyboard and wood fiber mills. This industry is only beginning in Latin America, largely in previously logged areas, as plyboard mill operators find that they can successfully handle many of the woods which were uncut or used only for charcoal.

The volume of timber being cut in the West Indian islands has rapidly decreased in the last few years. In Cuba, almost all of the accessible forest has been heavily culled so that little sizable timber of the better-selling kinds is available. During a four-year period (1946–50), when world economic conditions were favorable for expanding markets, lumber production in Cuba dropped more than 200,000,000 board feet, while imports increased by more than 30,000,000 board feet (Smith, 1954). In 1951, the production of *cedro* lumber exceeded in volume all other hardwoods cut. The total production of *Cedrela* lumber was 3,226,893 board feet, with an average value per thousand board feet of $300, a value equaled only by *caoba* or mahogany, which is widely exported.

In Mexico, the production of *Cedrela* lumber is equally high. For the period from 1938 to 1941, the total authorized production of *cedro* lumber in five Mexican states varied between 12,814 and 16,453 cubic meters. This does not take into account the vast amount of unauthorized cutting by small operators. In December, 1957, the sawmill at Donaji (formerly Tollosa), Oaxaca, was hauling logs of second choice hardwoods for distances of more than 10 kilometers through the forest over the roughest kind of terrain. Here the nearest *cedro* of harvestable size is too far back in the hill country to make cutting profitable. Throughout this area, there is reproduction of *cedro* in the most recently harvested sites, but even the small trees which had reached six to eight inches in diameter had been harvested before they

had produced a full seed crop. One old gentleman in this area had planted in Palomares in 1942 a stand of *Cedrela* seedlings, which he had brought in from the surrounding forest. This stand is now an estimated 70 feet tall with trunk diameters (DBH) of 20 inches and more. The trees are fruiting heavily and can supply seed for replanting *C. odorata* in the area.

In Panama, cutting of hardwoods is the same highly selective individual logging to cull the more valuable sorts which is prevalent in other areas of Latin America. Along the Chagres River, mahogany is removed first, *cedro* second, and other hardwoods in order of their decreasing value on the market. These are floated to mills on the shore of Madden Lake. In the Canal Zone, where the cutting of trees is restricted (some poaching was noted within the Zone in a little used part of a military reservation), *Cedrela* is a common tree in the second growth forest. On the Pacific slope this is *C. angustifolia*, while *C. odorata* is more common on the Atlantic slope.

Veillon (1955) reports that mahogany and *cedro* are the most desired timbers in the state of Barinas, Venezuela. In 1939, only these two kinds were being cut. After 1944, other kinds were being used. In 1949, Barinas produced 39 per cent of the timber cut in Venezuela. Of this, 67,746 cubic meters were *cedro*. From 1951 to 1954, *cedro* formed 43 per cent of the output of Barinas mills. This was a total production of 82,448 cubic meters, which sold at 180 to 210 bolivars a cubic meter at nearby towns. Where it is available, *cedro* is being cut in roughly this same proportion throughout Venezuela. As elsewhere, the most valuable timber is removed at first, and second choice timbers are gradually harvested. Little effort is being made to replace stands on a continued yield basis. The government of Venezuela is growing seedlings of many forest trees for distribution, but those nurseries which I saw at Maracay and Merida had only a few thousand trees in stock (pl. 13). This would not seem sufficient to replace the annual cut of these valuable trees.

Cedrela has frequently been used as cover for coffee plantations because of the ease with which it may be started as well as its ultimate value as a source of lumber. In many areas of Latin America, it is widely planted on the streets. Its open crown provides moderate shade, it is resistant to the hard usage which street plantings frequently receive, and it is resistant to insect and fungus injury. Its major insect enemy seems to be a borer (*Hypsipyla grandella* Zell) (Bascopé *et al.*, 1957).

Habit

Cedrela occurs throughout the American tropics as trees which may grow to considerable stature. The trunk is usually free of limbs and sprouts for at least a single log length (16 feet) if the tree grows in the open. Those developing under forest conditions may develop trunks free of branches to a height of 75 or more feet above the ground. As these trees rarely develop greatly extended buttresses (they may be buttressed to a height of 5 or 6 feet) almost the entire bole length is available as lumber.

Branching in *Cedrela* is open and the branches are often long and straight so that the crown is a well-formed globe or umbrella shape of moderate density. It is frequently difficult to collect botanical specimens as the foliage is borne largely at the outside of the crown far out of reach from the ground. In areas with a marked dry season, all of the foliage is shed for a part of the year. In those areas where the rainfall merely diminishes somewhat during the "dry" season, leaf fall occurs primarily just before the new flush of growth appears.

While *Cedrela* trees may occur as scattered individuals in undisturbed forest where their crowns are in the canopy, they are far more numerous in areas of second growth forest where mature trees with their crowns in the canopy and seedlings with their crowns in the understory may occur in groups. They are frequent along fence rows and along roadsides when there is a seed tree nearby.

Almost all of the naturally occurring *cedro* is found on well-drained soil. The trees seem to be highly tolerant of differences in soil *p*H as I have seen the same species on acidic volcanic soils in southern Mexico and alkaline limestone soils in Panama. While they respond well to rich soil, *cedro* trees seem to be very intolerant of poorly drained situations. Even on the poorest of rocky soils, they will attain good size, with at least a full log length of clean bole. Trees growing on steep hillsides are less desirable for lumber for they apparently develop a heavy compression wood on the downhill side.

Foliage

All of the American species of *Cedrela* have alternate, paripinnate leaves clustered at the ends of the twigs. While leaflet pairs vary considerably in their placement, they usually are oppositely arranged in mature foliage. Foliage from different parts of the same tree varies widely in leaf length, leaflet number, size and shape of leaflets and indument.

Leaflet venation in the more commonly encountered weedy species, *C. odorata* and *C. angustifolia*, tends to be irregular, with widely spaced, arcuate secondary veins. In *C. Lilloi*, *C. fissilis*, and to some extent in *C. montana* and *C. oaxacensis*, the secondary veins are close together and very regularly placed parallel to one another. There are 9 to 14 pairs of secondary veins per leaflet; variation in number of pairs of secondary veins depends upon the size of the leaflet and is of no significance taxonomically.

Leaflets of *Cedrela* species were cleared and stained by Dr. Howard Arnott for microscopic examination. Pubescence is of two kinds on the foliage. In many species puberulence is restricted entirely to the veins and venules. While this is apparent with a hand lens, in cleared material the puberulence, formed by short outgrowths of the surficial cells, is easily overlooked. These projections sometimes appear to be solely a part of the epidermal cells, although the larger of these represent a single cell in themselves. In those species of *Cedrela* which are distinctly pubescent or hirsute, the trichomes are sometimes restricted to the veins and venules. Often they are borne on the entire under surface of the leaflet. These are multicellular uniseriate trichomes with a distinctive basal cell; the shaft of the trichome gradually tapers to an acute apex. In *Cedrela fissilis* and *C. montana* particularly, the basal cell of the trichome is surrounded by a ring of small cells. The "nail-head" appearance is due to the shape of the basal cell.

Cross sections of the leaf tissue of the species of *Cedrela* show no anomalous structures. There is only a single palisade layer and a single upper and lower epidermis. In all of the species, the stomata are of the ranunculaceous type of Metcalfe and Chalk (1950). While glandular hairs are reported for *Cedrela*, the reference must be to Old World species formerly included in the genus as no glandular hairs have been found in the species under consideration in this paper. Secretory cells in the leaf tissue are restricted almost entirely to the vascular bundles. Some few secretory cells were observed in the palisade parenchyma in *C. angustifolia* and *C. fissilis;* they are rare outside of the vascular tissue in the other species. Crystals are abundant in the vascular tissue of the leaf of *C. odorata*. In all of the species, the vascular strand is bicollateral; a sheath of regularly shaped parenchyma cells surrounding the strand forms an extension of parenchyma tissue to both the upper and lower epidermis, and the epidermal cells at the point of contact are smaller than over the remainder of the leaf surface.

Villaça and Ferri (1954) have commented on the type of guard cell present in leaves of *Cedrela fissilis*. All of the species of *Cedrela* have the same kind of guard cell, in which a dumbbell-shaped lumen contains the cytoplasmic contents. While it is difficult to determine in dried material, apparently the closing of the stomatal aperture is partially effected by the lumen, which expands between the two bulbous ends and forces the adjacent wall outward into the opening. Epidermal preparations of *C. montana* clearly showed this in several stages. When fully closed, these stomata appear as two nearly semicircular guard cells enclosing closely parallel bars when the canal has expanded to a diameter nearly equaling that of the bulbous ends of the lumen. They are obviously not of the same derivation as the guard cells of the Gramineae to which Villaça and Ferri liken them, as there are no contiguous or parallel subsidiary cells present. In all other aspects the stomata of *Cedrela* are the anomocytic type (type A) of Metcalfe and Chalk (1950). In none of my epidermal preparations could I find the obturating cells described by Villaça and Ferri.

Pollen samples of all of the American species of *Cedrela* were prepared following the technique recommended by Erdtman (1952). All of the samples were 4-colporate, prolate spheroidal. Pollen from different species of *Cedrela* shows no distinguishing surficial marks. While there was a size difference observable in the few samples prepared, insufficient numbers of samples were studied to ascertain validly the average size of pollen grains for each species.

Details of the leaf and pollen anatomy are so uniform throughout the species of *Cedrela* that they have little taxonomic value. From field experience, it is known that pubescence is of doubtful use in delimiting taxa in the genus. Microscopically, the enlarged "nail-head" appearance of the basal cells of the trichomes is of no value as it is present to a certain degree with all of the large uniseriate trichomes. The densely crystalliferous nature of the vascular tissue of the leaf of *C. odorata* is probably a good character to differentiate this species from *C. angustifolia*, but this is of little use to foresters who need criteria easily usable in the field.

Inflorescences

The species of *Cedrela* all bear paniculate racemes at the apex of the branchlets. In *C. odorata* and *C. angustifolia*, the inflorescence is usually open. The secondary and tertiary branches of panicles of *C. fissilis* and *C. montana* may be so foreshortened that the flowers

are crowded. There is such a wide variation in the size of the inflorescence and in the number of flowers in an inflorescence that these differences cannot be referred to species. In all of the species, the inflorescence is pyramidal in general outline.

Flowers

Cedrela flowers are perfect and have a double floral envelope. The calyx is variable within the species, but general calyx forms are specifically distinct. *C. odorata* has a cup-shaped, usually glabrous calyx with an irregularly toothed margin. *C. angustifolia* usually has a puberulent, regularly 5-toothed calyx. These differences are reliable so long as infraspecific variation is minimal; unfortunately the toothing of the calyx of *C. angustifolia* may be somewhat irregular, while the calyx of *C. odorata* may be distinctly and evenly 5-toothed in trees from areas where these two species make contact. Calyx characters in the remaining *Cedrela* species are generally distinctive. Here again, where *C. oaxacensis* and *C. angustifolia* grow in proximity in Central America, the deeply 5-lobate calyx form of the former species may be seen in flowers of the latter species.

Petals of all of the species of *Cedrela* are about three times as long as they are wide, and densely pubescent or puberulent without. They are attached to the gynophore along the lower third of their length by a carina. The relative thickness of the petal tissue varies from species to species and some of the species have a heavily pigmented area around the apical margin. None of these differences is so marked as to be critical.

The androecium consists of five stamens. The paired anthers are dehiscent throughout their length and, as the connective is usually massive, the sacs are oriented so that the pollen is discharged toward the center of the flower. In all of the species, the filament is adnate to the gynophore as far as the base of the ovary. The connective is continued into a small apiculum in some species.

The ovary is conical to subglobose, puberulent without and divided into 5 (4) locules within. The numerous hanging ovules are arranged in two rows in each locule. The style culminates in a capitate stigma in which the stigmatic surface is confined to the margins and lower side. The style in *Cedrela* is fleshy and may be somewhat angled or fluted in the dried condition. While there appear to be some specific differences in ovary shape and stigma thickness, these are not constant enough to be of taxonomic value.

Fruit

The fruit of *Cedrela* is a septicidally dehiscent capsule borne near the ends of the branches of the inflorescence. The capsule dehisces from the apex to the base, exposing the many winged seeds which lie along the central column between wings which extend from the base to, or nearly to, the apex. Reference has frequently been made in the literature to the shape of the seed wings as a taxonomic character. Unfortunately, the shape of the wings on the seeds of *Cedrela* is entirely dependent upon the number of seeds maturing in each cavity and thus upon the amount of space available for the developing wing tissue. The apex of the column has a broad area of different appearance from the remainder of the column tissue. This remains constant in its general configuration and markings for each species. The size of the capsule is an unreliable taxonomic character except in *C. oaxacensis*, which bears the largest capsules in the genus. Even here, though, the smaller capsules of this species may be confused with the larger capsules of *C. angustifolia*, although the capsules of the latter species are usually thinner-valved.

Valve thickness is more nearly constant for a species than overall capsule dimensions. The capsules of *C. fissilis* have thick valves in all of the specimens examined. The valves of the capsule of *C. odorata* are thin. These provide supplementary characters of value in specific determination.

Thus, it becomes obvious that the plant has few parts which provide reliable characters for separating the species of *Cedrela*. For positive identification of a specimen from an area in which intermediate forms are found, foliage, flowers and fruit are all desirable. Only by using a combination of these can any surety of judgment be maintained. A combination of foliar and calyx characters is, perhaps, the most helpful. Foliar plus fruit column characters are usually sufficient if the specimen is not from a tree of intermediate characteristics. For specimens of an intermediate type, an evaluation of all of the information available may not be sufficient to place the taxon clearly.

Preparation of Data

The above information on the value of morphology of various plant parts in *Cedrela* is based upon a detailed examination of many specimens. The many species names used for material in herbaria have badly confused the taxonomy of the genus. Recently there has been so much emphasis on the great value of statistical studies in

evaluating the specific differences in badly confused groups, that I attempted an Andersonian approach, using specimens available in the larger herbaria of the United States. Selecting 25 characters which could be measured, counted, or otherwise scored, I measured, counted, or otherwise scored 360 herbarium specimens chosen without regard to label data. For convenience, these were roughly grouped by obvious characters before analysis so that selection of similar data for final manipulation would be easier. For over two years, this was continued at odd intervals, so that there was certainly no consistent bias toward one character or another. This resulted in some very impressive sheets of figures.

Armed with these data, I then approached the accounting department of the Academy of Natural Sciences of Philadelphia to borrow a calculator which would manipulate the data. By following many suggested formulas and assembling many means and ratios, including a leaflet length–width ratio and a flower length–calyx length ratio (which really looked interesting), I arrived at a startling conclusion. With current herbarium material, one cannot statistically distinguish the species of *Cedrela*. For those who are statistically inclined, the confused *C. mexicana–C. odorata* group was analyzed from 168 specimens and nearly 4200 separate evaluations were produced, showing that no specimen here was distinct from any other in this group and proving—I hope—that these are the same species.

In a consideration of tropical American genera, specimens are frequently lacking from large areas in the expected geographic ranges of species, including those of considerable economic importance. Also, the available collections have all too frequently been selected because the plant happened to be readily available; there have been few attempts to document the variability of a plant in one area or colony until this information has become important for monographic interpretation. For these and numerous other reasons (such as the unknown genetic background of the bulk of the tropical woody flora), I cannot confidently support the segregation of subspecific entities within a species in *Cedrela*.

The unknown genic background of *Cedrela* probably hides the reason for the confusion in differentiating the species. The only available chromosome count for *Cedrela* (Simmonds, 1954) was reported as $2n=50–52$ for a specimen reported under the name *C. odorata*. Dr. O. J. Eigsti has been unsuccessful in making counts on cytological material which I collected. From the variability in even-aged trees of *cedro* in second growth forest (see pl. 14) I suspect that

Cedrela may represent a polyploid series. Each tree exhibits such wide variation in foliar characters that more than one "species" can frequently be picked from the same individual. While a casual examination of herbarium material gives the impression that one species intergrades with the next, an attempt to evaluate the specimens statistically leaves no doubt that *C. odorata* intergrades with *C. angustifolia*, that this species intergrades with *C. oaxacensis* in Central America and with *C. fissilis* in South America, and that *C. fissilis* intergrades with *C. Lilloi* to a lesser extent. This latter impression may be due to lack of collections of intermediate forms, as there are few herbarium specimens of *C. Lilloi*. Only *C. montana*, restricted to higher elevations in northwestern South America, seems to remain relatively distinct, but even here there are indications that some mixing with *C. angustifolia* may occur where the latter has been introduced at higher elevations. Every indication from field observation and from herbarium specimens points toward the complete interfertility of all of the species of *Cedrela*.

Fossil Record

Not only is present-day *Cedrela* variable, but abundant fossil material properly referred to *Cedrela* by Roland Brown (1937) shows an equally variable habit. Brown (l.c.) has summarized the available information, which shows a wide distribution of fossil *Cedrela* throughout the western United States from upper Oligocene to early Pliocene. Fossils reported as *Cedrela* by Berry (1916, 1930) from the Eocene of the southeastern United States do not appear to be correctly identified. I suspect that these are individual leaflets of *Schinus* or simple leaves of yet another genus. However, Berry (1930) illustrates a compound leaf (pl. 36, fig. 7) which has all of the general characteristics of a leaf of *Cedrela*. This he has called *Sapindus formosus*. A detailed study of the original Berry specimen is indicated, as a widespread occurrence of *Cedrela* in the Oligocene indicates a prior distribution. Such an adaptable and variable plant as *Cedrela* is certainly to be expected among the assemblage of genera reported for the Eocene of the southeastern United States.

Unfortunately, the variation encountered in the foliar anatomy of present-day species of *Cedrela* leaves little hope that detailed study of the foliar anatomy of fossil *Cedrela* will aid in the differentiation of fossil species. As Brown (l.c.) has already indicated, the morphology of detached *Cedrela* seeds will be of little value. Thus, the differentiation of *C. merrilli* (Chaney) Brown from the Oligocene in

Oregon, *C. oregoniana* (Lesquereux) Brown from the Miocene and lower Pliocene(?) of Oregon and Idaho, and *C. pteraformis* (Berry) Brown from the Miocene of Washington appears to be as sound as can be expected. Later, Brown (1940) recognized *C. lancifolia* (Lesquereux) Brown from the Miocene of Colorado.

Systematic Treatment

CEDRELA P. Brown

Cedrela P. Brown, Civil and Natural History of Jamaica 158. 1756. *Cedrus* Mill. Gard. Dict. ed. 7. 1759. *Johnsonia* Adans. Fam. 2: 343. 1763. *Pterosiphon* Turcz. Bull. Soc. Nat. Mosc. 1: 589. 1863. *Surenus* O. Ktze. Rev. Gen. Pl. 1: 110. 1891.

Trees to 60 meters tall, with fissured gray or brown bark and pyramidal or spreading crowns. Trunk buttressed on old and large trees. Branchlets green or brown, sometimes conspicuously lenticellate. Leaves alternate, paripinnately compound, very variable in length; leaflet pairs variable in number, 8 to 20 pairs, opposite or subopposite; leaflets ovate to lanceolate, generally acuminate, glabrous to densely pubescent, margin entire, very variable in size and shape. Inflorescence terminal, pyramidal, paniculate, branches generally at right angles to the axis. Bracts caducous to subpersistent, deltoid or lanceolate. Flowers pedicellate to subsessile, perfect. Calyx cup-shaped and split on one side to completely 5-lobed, membranaceous. Corolla of 5 (4–6) distinct spathulate to lanceolate petals usually adnate to the gynophore along the lower third, entire, frequently fleshy, variously pubescent. Stamens 5, with fleshy filaments adnate to the gynophore below, free above, as long as or shorter than the corolla; anthers discharging introrsely through a slit the entire length of the anther sac, connective frequently prolonged into an apiculum. Pistil borne at the apex of the gynophore; ovary 5-locular, multiovulate, pubescent; ovules hanging in two rows per locule on the central column; style arising gradually from the apex of the ovary, pubescent, fleshy; stigma capitate. Fruit a septicidally dehiscent capsule opening cleanly from the apex; seeds hanging from the thick central column, numerous, the seed coat continued as a membranaceous wing from the apex of the seed.

Trees of the American tropics from Mexico to Argentina including the West Indies. They are restricted almost exclusively to well-drained habitats and may occur in deciduous forest or lowland and montane rain forest. Since the trees have been so widely cut for lumber, it is now impossible to ascertain the former natural distribution and frequency of occurrence of several of the species. Both *Cedrela odorata* and *C. angustifolia* have been widely distributed by man both as decorative trees and as reforestation subjects. These two species are common throughout their range in second growth forest, where they may occur as groups of even-aged trees. They may also seed themselves along fence rows in pastures and along roadsides.

The following key is not intended to be a "natural" key or to show any phylogenetic relationships. The species of *Cedrela* are so closely allied, and the morphological characteristics are so similar that it is impossible to distinguish a more primitive or a more advanced species.

KEY TO SPECIES

A1. Calyx cup-like, split on one side, variously dentate.....B
A2. Calyx regularly and deeply 5-lobate.....D
B1. Leaflets glabrous to puberulent beneath, very rarely hirsute except along the midrib and secondary veins.....C
B2. Leaflets generally hirsute beneath, rarely merely puberulent.....*C. fissilis*
C1. Leaflets strongly oblique at the base, often glabrous; calyx usually glabrous, irregularly dentate; petals thin, evenly light in color; column in capsule with wings extending to the base of the broad apex.....*C. odorata*
C2. Leaflets slightly oblique at the base, puberulent to pubescent particularly along the veins beneath; calyx puberulent, generally regularly 5-dentate; petals moderately thick, often darker in color at the apical margin; column in capsule with wings extending to the base of the narrow apex. *C. angustifolia*
D1. Leaflets abruptly acute at the base, usually glabrous.....*C. Lilloi*
D2. Leaflets never abruptly acute at the base, pubescent.....E
E1. Calyx 1–1.5 mm. deep; pubescence beneath the leaflets frequently light in color.....*C. oaxacensis*
E2. Calyx 1.5–2.5 mm. deep; pubescence beneath the leaflets tawny to dark in color.....F
F1. Gynophore thin in relation to length; trees of elevations of less than 300 m. in southern South America.....*C. fissilis*
F2. Gynophore stout in relation to length; trees of elevations above 1200 m. in northwestern South America.....*C. montana*

Cedrela Weberbaueri of Peru is known from only two collections, which may not be conspecific. This species cannot be keyed out on the basis of fruit, and no flowers are known. Until better material is available, no satisfactory disposition can be made of this name. A short description will be found at the end of the treatment.

Cedrela odorata L. Syst. Nat. ed. 10: 940. 1759. *C. guianensis* A. Juss. Mem. Mus. Hist. Nat. Paris 19: 295. 1830. *C. mexicana* Roem. Syn. Monogr. 1, Hesper. 137. 1846. *C. Velloziana* Roem. l.c. *C. Brownii* Loefl. ex O. Ktze. Rev. Gen. Pl. 1: 111. 1891. *Surenus Brownii* (Loefl. ex O. Ktze.) O. Ktze. l.c. *Cedrela occidentalis* C. DC. & Rose, Contr. Nat. Herb. 5: 190. 1899. *C. mexicana* var. *puberula* C. DC. Bull. Herb. Boiss. ser. 2, 5: 427. 1905. *C. Sintenisii* C. DC. Ann. Conserv. Jard. Bot. Genève 10: 169. 1907. *C. yucatana* Blake, Proc. Biol. Soc. Wash. 33: 110. 1920. *C. longipes* Blake, Contr. Nat. Herb. 24: 9. 1922. Plates 7, 13.

Tree to 40 m. (fide *A. C. Smith 3585*). Branchlets generally glabrous, occasionally conspicuously lenticellate, more often with small lenticels. Leaves with 5 to 11 pairs (usually 6 to 7 pairs) of leaflets 8 to 17 cm. long by 2.5 to 5.5 cm. wide (usually 10.5 by 3.5 cm.), broadly lanceolate to ovate, base acute to rounded, often markedly oblique, apex acuminate, obtuse, rarely acute, sometimes mucronulate, generally glabrous, occasionally puberulent or short pubescent along the veins beneath. Inflorescence open, variable in size, often shorter than the leaves, usually glabrous, rarely puberulent, bracts caducous. Flowers 6 to 9 mm. long; calyx cup-shaped and split on one side, 1.5 to 3 mm. deep, margin generally shallowly and irregularly toothed, glabrous, rarely puberulent, light to dark in color; petals elliptical to subspathulate, puberulent without, uniformly light in color; filaments thick but usually of uniform diameter; anthers short apiculate, 0.75 to 1.5 mm. long; ovary hemispherical to ovoid, usually glabrous, 1 to 2 mm. long, style 1 to 2.5 mm. long, usually glabrous, capitate stigma about 0.5 mm. thick. Fruit 2.5 to 4.5 cm. long, valves thin, central column with wings extending to the base of the broadened apex.

Trees of dry to moist soils at lower elevations, frequent in second growth forest but generally cut in the West Indies and Central Amer-

MAP 1. Distribution of *Cedrela odorata*.

ica before they become very large; ranging from northern Mexico and the West Indies to the Amazon drainage of Brazil.

Cedrela odorata L. is the earliest binomial proposed in the genus. It thus becomes the type for the genus and the type for the species is

Patrick Browne's illustration (pl. 10, fig. 1, The Civil and Natural History of Jamaica, 1756; see discussion, p. 297). Linnaeus cites no dried specimen for the name (10th ed. Syst. Nat.). He does, however, cite Peter Loefling (Iter Hispanicum eller Resa . . . p. 183, 1758), who describes the genus *Cedrela* and notes that he saw trees at Cumana (Venezuela) and Trinidad. The status of the *Cedrela* species suggested by O. Kuntze as proposed by Loefling will be discussed later.

Adrien de Jussieu provided an ample description for *Cedrela guianensis* which places it without question as a part of *C. odorata* L. While de Jussieu did not cite a specific collection, I have before me a collection of *Cedrela* made by Joseph Martin in French Guiana. The label apparently is in Jussieu's hand and the specimen constitutes an authentic representation of his concept.

For many years, *Cedrela mexicana* Roemer has persisted in the literature as a separate entity. Field experience in forestry plantings and nurseries and collections from trees purported to be *C. mexicana* as distinct from *C. odorata* led directly into this revision. The Roemer name is based on a collection cited "Mexico in silvis Papantlae," following the literature citation, "*C. odorata* L? Schlecht. & Cham. in Linnaea 6: 422," which obviously refers to a Schiede collection. *Deppe & Schiede 1304* at the New York Botanical Garden is, thus, an isotype. Consisting of only two leaves, it fits the description completely, including the scattered puberulence noted by Roemer. From the herbarium of the Leningrad Botanical Garden, I have seen an ample holotype specimen which leaves no doubt that *C. mexicana* Roem. is synonymous with *C. odorata* L. While the bulk of the collections of *C. odorata* L. are glabrous or glabrate this variant probably arises from the cross-breeding between species which is apparent in the genus, and pubescence is certainly to be expected wherever *C. odorata* comes into contact with *C. angustifolia*, as it does in the area of the type locality of *C. mexicana* in Vera Cruz.

At the same time, Roemer published *C. Velloziana*, citing the Vellozo plate 67 for *C. odorata* and locality as near Rio de Janeiro. In 1878, in Martius' *Flora Brasiliensis* Casimir De Candolle cited a single collection, *Allemao 60*, under this name. From a photograph of the specimen at Geneva, it is evident that it coincides with Roemer's description and I accept this as a lectotype for the name *C. Velloziana* Roemer. However, Roemer's description and the specimen bring *C. Velloziana* well within the variation to be found in *C. odorata* and it is, therefore, a synonym.

In 1891, O. Kuntze (Rev. Gen. Pl.) published the combination *Cedrela Brownii* which he equated with *C. odorata* L. so that he could make a transfer of the specific epithet to *Surenus*. This is the only name for which Kuntze provided sufficient reference to literature to make a valid transfer (see p. 299). However, Loefling never intended this as a specific name, but merely a reference to Patrick Browne's earlier publication describing the genus. This is supported both by the heading for this section of the *Resa* (p. 177, "Plantae Americanae —Sectio I: ma. Genera Nova."), and by the period and space separating *Cedrela* and *Brownii* (p. 183). This is further supported by the general lack of specific entries throughout the remainder of this section. I heartily agree that this name belongs in the synonymy of *Cedrela odorata*.

Cedrela occidentalis C. DC. & Rose represents one of the intermediate groups of specimens which contribute to the difficulty in drawing species boundaries in *Cedrela*. Certain obvious characters such as the shape of some of the leaflets of *Rose 1438* as well as their puberulence suggest *C. angustifolia*. On the other hand, the rather broad apex to the column in the fruit, the glabrous or nearly glabrous calyx and the thinner petals show closer affinities with *C. odorata*, where I am placing the species *C. occidentalis*. The original description errs in stating that the teeth of the calyx are as long as the tube (they are shorter) and that the anthers are not apiculate (while it is short, the prolongation of the connective is present between the upper ends of the anther sacs). While no type was designated by the authors, *Rose 1438* satisfies the description of *C. occidentalis* and I select this as lectotype because it includes both flowers and fruit, as well as a full range of foliar variation, from nearly lanceolate leaflets with oblique bases to nearly ovate leaflets with slightly oblique bases. Incidentally, Rose violated leg b. of his key (Contr. Nat. Herb. pp. 190, 191) in placing *C. occidentalis* here as both the Rose and the Palmer collections are definitely pubescent on the lower leaf surfaces.

Casimir De Candolle proposed *C. mexicana* Roem. var. *puberula* in 1905 based on a collection which he cites as *Pittier 13507*. The type, in fruit, is well within the limits of variation of *C. odorata* and is thus placed in synonymy here. The specimen is actually a Tonduz collection number (*13507*) in herbarium Pittier from Costa Rica.

Material of *C. odorata* L. from Puerto Rico collected by Sintenis has larger and more darkly colored leaflets than are generally found in West Indian collections of this species. C. De Candolle segregated

this material as *C. Sintenisii* in 1907. Because this variation, while seemingly restricted geographically, is to be seen in occasional collections from Guadeloupe and in several collections from Jamaica, I place it in synonymy. It is certainly well within the overall range of variation of *C. odorata* when mainland material is considered. De Candolle did not designate a type; as *Sintenis 3981* seems to be generally distributed and fits the description, I select this collection as lectotype.

Pubescence in *Cedrela* is not a constant character. Although *C. odorata* is more nearly glabrous than any of the other West Indian and Central American species, many collections from the West Indies show more or less puberulence even though the more pubescent *C. angustifolia* does not occur there and thus cannot contribute pubescence to the populations of *C. odorata*. On the mainland of North America, *C. angustifolia* and *C. odorata* occur in the same areas. It is obvious from the herbarium material and from field observations that intermixing of these two species has occurred. *C. yucatana* Blake shows the development of puberulence on the foliage, the leaflet broadening and the more pubescent floral parts in the Schott collection from Merida, Yucatan, cited as the type by Blake. On the other hand, *Goldman 505* from Apozote, Campeche (cited with the original description), is glabrate, the leaflets are lanceolate and the fruit has the broad column apex typical of *C. odorata* in the West Indies. Again, the nearly glabrous calyx, the thinner petals, and the very oblique base of the leaflets place the type collection of *C. yucatana* in *C. odorata* rather than in *C. angustifolia*.

C. longipes Blake is an example of the wide variation to be found in the species of *Cedrela*. On the basis of foliar shape and size, the type collection, *Whitford & Stadtmiller 30*, agrees almost exactly with *C. Dugesii* and *C. ciliolata*, which I have placed in synonymy in *C. angustifolia*. Yet the leaflets of this collection are completely glabrous and the venation is much less regular; on the other hand, the foliage is unlike the lanceolate, oblique-based leaflets of many collections of *C. odorata*. The flowers of *C. longipes* were compared detail for detail with the flowers of *C. angustifolia* (the entities *C. Dugesii* and *C. ciliolata* previously referred to). The calyx of *C. longipes* is minutely puberulent and shallowly and unevenly dentate; the other entities have pubescent calyces which are regularly dentate or lobed. The connective of the stamens is narrow and inconspicuous in *C. longipes;* in the others it is relatively wide and conspicuous. Unfortunately, size comparisons in flowers of *Cedrela* are invalid because of the wide variation in the same inflorescence be-

tween flowers in different stages of anthesis. There were no valid differences discernible in the petals. Because the glabrous surface and venation of the leaflets and the characters in the calyx and stamens of *C. longipes* agree completely with those of *C. odorata* and not with those of *C. angustifolia*, I am placing it in the synonymy of *C. odorata*. Had other collections with the same characteristics been found in neighboring areas of Central America, there would have been reason for maintaining this as a separate specific entity. This collection assuredly represents variation in an individual species.

SPECIMENS SEEN

MEXICO.—San Luis Potosi: Tamazunchale, *C. L. & A. A. Lundell 7276* (fl.), July, 1937 (NY). Sinaloa: Coacoyolitos, Rosario, *Ortega 5860* (fr. immature), Nov., 1925 (PH). El Roble, Mazatlán, *Ortega 6532* (fl.), Dec., 1926 (PH). Mazatlán, *Ortega 6774* (fr.), March, 1931 (F). Escamillas, Mazatlán, *Ortega 6346* (fl.), Aug., 1926 (F, MO, PH). Choix, Tasajera, *Ortega 899* (fl.) (F). Tepic: *Palmer 1854* (fr.), Jan. 5–Feb. 6, 1892 (F, NY). Rosa Morada, *Nelson 4357* (fl. & fr.), June 23, 1897 (US). Acoponeta, *Rose 1438* (type coll., *C. occidentalis* C. DC. & Rose) (fl. largely past anthesis), June 23, 1897 (F, GH, MO, NY, US). Jalisco: Tuxpan, *Mexia 1035* (fr. immature), Nov. 4, 1926 (F, GH, MO, NY). Michoacan: Coalcoman, *Hinton 13877* (fl.), July, 1939 (NY). Vera Cruz: Colipa, *Liebmann 91* (st.), 1841–43 (F, US). Papantla, *Deppe & Schiede 1304* (type coll., *C. mexicana* Roem.) (fl.) (LE, NY). Tabasco: Estapilla, Tenosique, *Matuda 3492* (fl.), June 18, 1939 (F, MO, NY). San Juan Bautista (Villa Hermosa), *Rovirosa 518* (fl.), July, 1889 (NY, PH). Campeche: Yohaltun, *Goldman 505* (fr.), Dec. 20, 1900 (US). Yucatan: Chichen Itzá, *Bequaert 105* (fl.), June, 1929 (F). Tuxpeña, *Lundell 925* (fr.), Nov., 1931 (A, F, GH, MO, NY). Suitun, *Gaumer 23380* (fl.), June, 1916 (F, MO, NY). Merida, *Schott 980* (fl.) (F). Oaxaca: Palomares, *Smith & Ruiz 3241* (fr.), Dec., 1957 (F, PH). Chiapas: Trapichito, Comitán, *Matuda 15966* (fl.), June, 1945 (F). Esperanza, Escuintla, *Matuda 18678* (fr.), Nov., 1950 (NY). Chicomuselo, *Matuda 4464* (fl.), July, 1941 (A, MO, NY).

CUBA.—Isle of Pines: *Curtis 325* (fr.), Feb., 1904 (F, MO, NY). Oriente: Bayate, *Ekman 5864* (fl.), June, 1915 (F); *Ekman 6157* (fl.), June, 1915 (MO). Monte Verde, *Wright 1152* (fl.), Jan.–July, 1859 (MO, PH); *Wright 1582* (fr.), Sept., 1859–Jan., 1860 (NY, PH). Las Villas: Belmonte, Cienfuegos, *Jack 7141* (fr.), March, 1929 (NY, US). Soledad, Cienfuegos, *Jack 7804* (fr.), March, 1930 (F). Havana: Santiago de las Vegas, *Wilson 2204* (fr.), Oct., 1904 (NY). Pinar del Rio: Cape San Antonio, *Roig 3251* (fr. immature), April, 1924 (NY); *Abarca 5141* (fl.), June, 1905 (F, NY). Matanzas: Rio Canimar, *Meisner Herb. 337* (fl.) (NY).

JAMAICA.—Hope Gardens, *Harris 11705* (fl. & fr.), Feb., 1914 (F, MO, NY, PH). Between Troy and Oxford, *Britton 668* (fr.), Sept., 1906 (NY); *Alexander s.n.* (fl.), 1850 (NY). Moneague, *Hunnewell 15296* (fl.), Feb., 1938 (GH).

HISPANIOLA.—Haiti: La Vallée, Tortue Island, *Leonard & Leonard 11514* (st.), Dec., 1928–Jan., 1929 (NY). Massif du Nord, Morne Pedregal, *Ekman 6140* (fl.), May, 1926 (NY). Morne Fourrise, *Ekman H-3828* (fl.), April, 1925 (US).

Massif des Matheux, St. Marc, *Ekman 8064* (fl.), May, 1927 (A). Cordillera Septentrional, Puerto Rata, *Ekman 14377* (fl.), March, 1930 (US).

PUERTO RICO.—Adjuntas, *Sintenis 3981* (type coll., *C. Sintenisii* C. DC.) (fl.), March, 1886 (F, MO, NY, PH). Between Adjuntas and Guayamilla, *Sintenis 4555* (fr.), June, 1886 (F, NY, MO, PH). Lares, *Sintenis 6001* (fl.), Jan., 1887 (NY, US). Luquillo, *Gregory 38* (fl.), May, 1940 (NY).

ANTIGUA.—*Rose, Fitch & Russell 3342* (fr.), Feb., 1913 (F, NY, US).

MONTSERRAT.—Roches, *Shafer 532* (fr.), Feb., 1907 (F, NY).

GUADELOUPE.—Basse Terre, *Duss 2315* (fl.), 1893 (F, NY).

MARTINIQUE.—Rivière Pilote, *Hahn 904* (fl.), June, 1869 (F, PH); *Sieber 55* (fl.) (B, MO, NY). Carbet, *Duss 1498* (fl.), 1881 (NY).

ST. LUCIA.—La Perle, *Box 2005* (fr.), Nov., 1938 (MO).

GRENADA.—St. Georges, *Broadway s.n.* (fr.), March, 1905 (F, NY); *Broadway s.n.* (fl.), June, 1906 (F); *Broadway s.n.* (fr. immature), Aug., 1906 (NY, MO).

TRINIDAD.—Woodbrook, *Broadway 5321* (fl.), July, 1924 (F, MO); *Broadway s.n.* (fl.), Aug., 1927 (MO); *Broadway s.n.* (fl.), June 17, 1932 (B, MO).

CURAÇAO.—Cas Cora, *Arnoldo 2090* (fl.), June, 1952 (US).

GUATEMALA.—La Libertad, *Lundell 3060* (fr.), April, 1933 (F). PETEN: Uaxactun, *Bartlett 12568* (fr.), April, 1931 (A, NY). SANTA ROSA: Near El Molino, *Standley 60705* (fr.), Dec., 1938 (F). Region of Capulín, *Standley 79657* (fr.), Dec., 1940 (F). SAN MARCOS: Near Malacatán, *Standley 68848* (fr.), March, 1939 (F).

BRITISH HONDURAS.—Corozal, *Gentle 219* (fr.), 1931–32 (GH, NY).

HONDURAS.—El Paraiso, *Whitford & Stadtmiller 30* (type coll., *C. longipes* Blake) (fl.), May, 1919 (GH). MORAZÁN: Zamorano, *Rodriguez 3051* (fl.), June, 1945 (A, F, MO). El Jacarito, *Standley 20486* (fl.), June, 1949 (F). Chahuite, *Standley, Molina & Chacón 5008* (st.), March, 1947 (F). COMAYAGUA: Las Limas, *Edwards P-363* (st.), June, 1932 (F).

EL SALVADOR.—San Martin, *Calderón 701* (fl.), May, 1922 (MO, NY).

NICARAGUA.—JINOTEGA: West of Jinotega, *Standley 10293* (fr.), June, 1947 (F). Cerro de la Cruz, *Standley 10952* (fr.), July, 1947 (F). CHINANDEGA: Chichigalpa, *Standley 11363* (fr. immature), July, 1947 (F).

COSTA RICA.—Nicoya, *Tonduz 13507* (type coll., *C. mexicana* var. *puberula* C. DC.) (fr.), Jan., 1900 (GH, NY [photo]). Alajuela, *Seibert 1600* (fr.), Oct., 1940 (MO). Between Belvedero and Taboga, *Brenes 12564* (fl. past anthesis), June, 1930 (F). Tilarán, *Standley & Valerio 46572* (fr.), Jan., 1926 (F).

PANAMA.—CHIRIQUI: Progresso, *Cooper & Slater 306* (fr. immature), July–Aug., 1927 (F, NY).

COLOMBIA.—Valparaiso, *H. H. Smith 1739* (fl.), March, 1898 (NY). BOLIVAR: Near Turbaco, *Killip & Smith 14348* (fr.), Nov., 1926 (F, NY).

VENEZUELA.—Sta. Lucia, *Curran & Haman 1095* (fl.), June, 1917 (GH, NY). FALCÓN: Riecito, *Mell s.n.* (fl.), July, 1923 (NY). MONAGAS: Cristobal Colon, *Broadway 486* (fr.), Feb., 1923 (GH, NY). DISTRITO FEDERAL: Caracas, *Pittier 9597* (fl.), June, 1921 (GH). Between Caracas and La Guaira, *Llewellyn Williams 12264* (fr.), Jan., 1940 (F, US). MIRANDA: Petare, *Pittier 7865* (fl.), May, 1918 (GH). CARABOBO: Between La Entrada and Las Trincheras, *Pittier 8886* (fl.), June, 1920 (GH, NY). MERIDA: La Victoria, *Smith & Jorgensen 3547*,

3548 (fr.), Jan., 1958 (PH). ARAGUA: El Consejo, *Ll. Williams 10694* (fr.), Nov., 1938 (F). El Limón, *Ll. Williams 10232* (fl.), June, 1938 (F, MO). TERR. DELTA AMACURO: El Palmar–Raudal trail, *Wurdack & Monachino 39721* (fl. & fr.), Nov., 1955 (NY). Between Curiapo & Pta. Cangrejo, *Wurdack 312* (fr. immature), April, 1955 (NY).

BRITISH GUIANA.—Swarima Is., Cuyuni River, *Forest Dept., field no. D-333* (fr. immature), Nov., 1932 (NY). Kanuku Mts., Moku-Moku Creek, *A. C. Smith 3585* (fr.), April, 1938 (F, MO, NY).

SURINAM.—Carel Francois, *Wood herbarium 103* (st.), Nov., 1942 (NY).

FRENCH GUIANA.—*Martin s.n.* (type coll., *C. guianensis* A. Juss.) (fl.) (F, NY, US); *Martin 450* (fl.) (F); *Sagot 1179* (st.), 1858 (MO).

ECUADOR.—ESMERALDAS: Quinindé, *Little 6257* (fl.), April, 1943 (NY).

PERU.—Lima, *Soukup 2176* (fl.), 1944 (F). Mouth of Río Santiago, *Tessmann 4639* (fl.), Nov., 1924 (NY).

BRASIL.—*Allemao 60* (fl. & fr.), (F [photo]). TERR. OF ACRE: Rio Macauhan, *Krukoff 5400* (fr.), Aug., 1933 (F, MO, NY). AMAZONAS: Humayta, *Krukoff 6218* (fl.), Sept.–Oct., 1934 (F, MO, NY, US). PARÁ: Belém, *Froes 11828* (fl.), 1940 (NY). Rio de Janeiro, (cult.), *Whitford 36* (fr.), June, 1918 (F, MO, NY); *Curran 343* (fr.), Nov., 1915 (GH).

BOLIVIA.—Beni, *White 2367* (fr. immature), Feb., 1922 (GH, NY).

Cedrela angustifolia Sessé & Moc. ex DC. Prodr. 1: 624. 1824. *C. brasiliensis* A. Juss. in St. Hil. Fl. Bras. Merid. 2: 86. t. 101. 1829. *C. paraguariensis* Martius, Flora 20, Beibl: 93. 1837. *C. paraguariensis* Mart. var. *brachystachya* C. DC. Monog. Phan. 1: 738. 1878. *C. paraguariensis* Mart. var. *multijuga* C. DC. loc. cit. *C. adenophylla* Mart. ex DC. pro syn. nomen nudum. loc. cit. *C. Glaziovii* C. DC. in Mart. Fl. Bras. 11-1: 224, t. 65, f. l. 1878. *C. Dugesii* S. Wats. Proc. Amer. Acad. 18: 190. 1882–83. *C. barbata* C. DC. Bull. Herb. Boiss. 2: 575. 1894. *C. imparipinnata* C. DC. in J. D. Sm. Bot. Gaz. 19: 4. 1894. *C. paraguariensis* var. *Hassleri* C. DC. Bull. Herb. Boiss. ser. 2, 3: 413. 1903. *C. caldasana* C. DC. Ann. Conserv. Jard. Bot. Genève 10: 170. 1907. *C. Mourae* C. DC. op. cit. 172. 1907. *C. Hassleri* C. DC. loc. cit. *C. longiflora* C. DC. op. cit. 173. 1907. *C. pachyrhachis* C. DC. op. cit. 174. 1907. *C. Balansae* C. DC. pro parte, Bull. Soc. Bot. Genève ser. 2, 6: 119. 1914. *C. rotunda* Blake, Proc. Biol. Soc. Wash. 33: 109. 1920. *C. Whitfordii* Blake, op. cit. 110. 1920. *C. ciliolata* Blake, op. cit. 34: 115. 1921. *C. Huberi* Ducke, Archiv. Jard. Bot. Rio de Janeiro 3: 189. 1922. *C. longipetiolulata* Harms, Notizblatt. 10: 179. 1927. *C. pacayana* Harms in Pilger, Notizblatt. 11: 784. 1933. Plates 8, 13, and 14.

Trees to 60 m. (fide *Krukoff 10724*), usually 30 m. or less, with upright branches and an open crown. Bark brownish or dark gray, deeply fissured. Branchlets with small lenticels, glabrous or glabrate. Leaves with 5 to 10 pairs (usually 6 to 8 pairs)

of leaflets. Leaflets 9 to 25 cm. long by 3 to 8.5 cm. wide (usually about 12 by 4.5 cm.), elliptical to ovate to ovate-lanceolate, seldom lanceolate, base subacute to rounded, slightly oblique, apex obtuse to long acuminate, acute, generally short acuminate, subacute; pubescent along the midrib above, scantily puberulent to thickly pubescent and scattered hirsute, primarily on the veins and venules below, sometimes glabrous or with axils of the secondary veins barbate. Inflorescence variable in size, often about equaling the length of the leaves, usually puberulent; bracts caducous. Flowers 6 to 9 mm. long; calyx shallowly cup-like and usually split at one side, 2 to 3 mm. deep, margin irregularly shallowly lobed to definitely 5-lobed, often scattered puberulent, dark in color; petals elliptical, densely pubescent, reddish near the apex; filaments fleshy; anthers apiculate, 0.8 to 1.9 mm. long; ovary 1 to 1.5 mm. long, hemispherical, puberulent; style 1.5 to 3 mm. long, thick, puberulent; capitate stigma about 0.5 mm. thick, glabrous. Fruit 2.5 to 5 cm. long, valves thin (to 1.5 mm. thick), central column with 5 conspicuous wings extending nearly to the narrow apex.

Trees of dry to moist sites at less than 2000 m. elevation, conspicuous in second growth before they are cut, ranging from northern Mexico to northern Argentina but absent from the West Indies as native trees. Frequently planted as ornamental trees and as shade for coffee plantings.

Cedrela angustifolia Sessé & Moc. ex DC. is widely distributed naturally as well as being a much used cultivated tree. Wherever a seed source is present, it appears in second growth forest in quantity, particularly on drier sites. Much of the success of *C. angustifolia* as a weed species appears to be in a genic assemblage which is very flexible. For this reason, also, the individuals of the species show a great diversity in all vegetative characters as well as an unusual variability in flowers and fruit. In areas of secondary forest where even-aged individuals occur, there are marked differences in the size and shape of leaflets, the placement, length and pubescence of leaves, and the form of the crown (pl. 14).

With all of the variability shown by individuals, there is no apparent means of separating geographically limited groups as distinct species or even varieties. A total of 57 collections of *C. angustifolia* representing its entire geographic range was tabulated for seven foliar characters and fifteen flower and fruit characters (whenever these were present). When no significant differences could be noted by inspection, leaflet length-width ratios and corolla-calyx length ratios were compared, with negative results. Since total leaf length and number of leaflets vary greatly with environmental differences, these could not be used. Variations in proportions of the androecium and gynoecium were, again, inconclusive. Casual inspection of the herbarium material would seem to belie the arithmetic, as collections

made in Brasil frequently have an entirely different aspect from those collected in Mexico.

In large part, the regional differences observable in *C. angustifolia* must be due to interbreeding of this species with other species of *Cedrela*. *C. odorata* is distributed over almost the same geographical area. From this species, *C. angustifolia* derives a more entire calyx

MAP 2. Distribution of *Cedrela angustifolia*.

margin, nearly glabrous, thin calyx, and narrower, nearly glabrous leaflets. The fruits of these two species are so close as to be almost inseparable, although the fruit of *C. angustifolia* tends to be larger and thicker-valved, with a more narrow sterile area at the apex of the placental column. When *C. angustifolia* interbreeds with *C. oaxacensis* in Central America, more deeply lobed calyx margins and a heavier fruit, as well as slightly broader, more pubescent leaflets appear in the *angustifolia*-like progeny. In the more southerly end of the range of *C. angustifolia* it intermixes with *C. Lilloi*, from which the product inherits narrower, more glabrate foliage and a more deeply lobed calyx margin, and with *C. fissilis*, from which there is derived greater leaf pubescence and calyx margin lobing. Interbreed-

ing with each of these species introduces more numerous and nearly parallel secondary veins in the leaflets.

Because of the wide variation in this species, there has been much confusion in nomenclature, not a little of which is due to the intergradations between species of *Cedrela*. The oldest name applicable to this taxon is *C. angustifolia*, published by Pyramus De Candolle in 1824 from the Royal Expedition material collected in Nova Hispania by Sessé and Mociño. The observable characters in the S. & M. drawing (photograph in Chicago Natural History Museum) clearly indicate the group to which this belongs. The calyx is cup-shaped and split at one side but the margin is more deeply lobed than that of *C. odorata*. The leaflets are proportionally somewhat wider and the base of each leaflet is less oblique than that of the leaflets of *C. odorata*. On the other hand, the calyx is not clearly and deeply five-lobed as it would be if the drawing depicted *C. oaxacensis*. Since no locality data were supplied with the De Candolle citation, this useful guide to the identity of the species is negated.

Adrien de Jussieu prepared the description of *C. brasiliensis* for St. Hilaire's *Flora Brasiliae Meridionalis*, basing it upon a St. Hilaire collection from Contendas, Minas Geraes. While I have neither original material nor a photograph, I have no hesitation in placing this name in the synonymy of *C. angustifolia* on the basis of the ample description and plate published by St. Hilaire in 1829. This is in spite of Casimir De Candolle's judgment in placing *C. brasiliensis* in the synonymy of *C. fissilis* Vell. (Monog. Phan. 1878). De Candolle obviously proposed a mixed concept in his interpretation of *C. fissilis*, as he cites *Sellow 1909* and *Andrieux 483* among the specimens of this species when he had already placed the Andrieux collection in his concept of *C. montana* var. *mexicana* in the same paper.

The specimen of *Cedrela* from Brasil on which Martius based the name *C. paraguariensis* has an entirely different general aspect. The foliage is smaller and thus not typical for any of the species of *Cedrela*. However, other Brasilian collections integrate this form into the general foliar pattern of *C. angustifolia* and, at the same time, indicate that this variation probably originates through intermixing with *C. Lilloi*. The flowers of *C. paraguariensis* leave no doubt of its true affinities. *Martius 78* stands as the type.

In his treatment of *Cedrela* in 1878, C. De Candolle places in synonymy with *C. paraguariensis* Martius the name *C. adenophylla*, which he attributes to Martius. I have found no description for this

name nor does De Candolle cite a published reference, so it must remain in synonymy as a nomen nudum.

At the same time, De Candolle proposed variety β *brachystachya* under *C. paraguariensis*. Although De Candolle subsequently treats the epithet *brachystachya* as a specific name in a key to *Cedrela* (Ann. Conserv. Jard. Bot. Genève 10. 1907), he cited no reference and the change in status is thus illegitimate. Examination of *Sellow 1907*, the type for the variety, shows no characters distinct from the characters of *Martius 78*, nor are there sufficient differences from the bulk of specimens of *C. angustifolia* to warrant its existence as a separate entity. De Candolle also published *C. paraguariensis* var. *multijuga* in this paper. The type (*Riedel 658* in the Leningrad herbarium) does not vary sufficiently to warrant varietal status.

Also in 1878, in the article on Meliaceae which he composed for Martius' *Flora Brasiliensis*, C. De Candolle erected *C. Glaziovii* on the basis of *Glaziou 6102*. While the specimen of this number which I have before me includes a leaf which is referable only to *C. odorata*, the small portion of inflorescence is typical of *C. angustifolia* as is the plant represented by the fine illustration (pl. 65, fig. 1) in *Flora Brasiliensis*. I therefore place *C. Glaziovii* in the synonymy of *C. angustifolia*.

In the mountainous area of west central Mexico in the states of Michoacan and Guanajuato, A. Duges and more recently Arsène have collected a series of specimens of *Cedrela* with an unusual leaflet form, although the flowers and fruit do not show differences beyond the expected variations in *C. angustifolia*. While I suspect that the leaflet form may be a generally stable character in a geographically delimited area, I hesitate to erect a subspecies or variety without searching the area for other forms of *C. angustifolia*. In both Duges' and Arsène's collecting techniques, such unusual specimens might have been selected from an abundant, more normal population. Therefore, I place both *C. Dugesii* Wats. and *C. ciliolata* Blake in the synonymy of *C. angustifolia*.

Glaziou's collection *11844* is one of the many intergrade forms which make the definition of *Cedrela* species so indistinct. The flowers show a more deeply lobed and heavily pubescent calyx, very reminiscent of *C. fissilis*, but in shape, venation and lack of tomentum the foliage is entirely that of *C. angustifolia*. Furthermore, the inflorescence has the more open aspect of the latter species. In 1894, C. De Candolle based *C. barbata* on this collection, but I find the

balance of the evidence points to the inclusion of this taxon in *C. angustifolia.*

De Candolle had been asked to study the Guatemalan collections of Meliaceae assembled by John Donnell Smith and he accordingly published *C. imparipinnata* in 1894 based on a fruiting collection (*J. D. Smith 2571*). These specimens fit well into the concept of *C. angustifolia.* The fragmentary specimen I have seen cannot be said to be imparipinnate.

In 1903, C. De Candolle published another variety on the basis of a specimen from Paraguay (*Hassler 5366*). *C. paraguariensis* var. *Hassleri* differs from well-developed *C. angustifolia* in its smaller leaves and shorter inflorescences, but the proportions and details of the flowers and the details of the foliage show its unquestionable place in *C. angustifolia.* Subsequently, De Candolle raised the varietal name to specific rank in 1907. Both of these names now are reduced to synonymy.

From the photograph of the type specimen of *C. Mourae* C. DC. it is apparent that this name must also be brought into the synonymy of *C. angustifolia.* Details of the flowers and leaflets show only the expected variation.

The same must be said for *C. pachyrhachis* C. DC., *C. longiflora* C. DC. and *C. caldasana* C. DC. In his 1907 article De Candolle places great emphasis on leaf and leaflet size and shape as well as on pubescence. In many tropical genera, such details are thoroughly unreliable, as anyone knows who has had field experience in the American tropics. In *Cedrela,* because of the interbreeding of species wherever they come together, these characters are especially unreliable. On one tree, it is frequently possible to find all of the combinations of foliar and pubescence characters known to occur within the limits of variation of the species throughout its geographic range.

C. Balansae was proposed by C. De Candolle in 1914. I have seen no material of *Balansa 2259* but I have ample material of *Hassler 11707,* which was cited as the type collection of this species by Buchinger and Falcone (1957). The specimen citation in the De Candolle article (1914, p. 121) is "*Hassler n. 1707*" and I assume this is a misprint for 11707 as I have found no Hassler specimens of *Cedrela* numbered 1707. The drawing of flower details and portion of a leaf published by De Candolle is presumably based on the Balansa collection. The long column and five-lobed pubescent calyx as well as the heavily pubescent leaf are characteristic of *C. fissilis* Vell. in some of its variants. On the other hand, *Hassler 11707* is in young fruit

stage and the specimens fall well within *C. angustifolia.* In fact, the ovate leaflet shape with an attenuate apex is nearly identical with that of the Duges and Arsène collections previously discussed. On the basis of the published figure and the Hassler collection, I feel that De Candolle was describing a mixed concept which must go into synonymy under both *C. fissilis* Vell. (*Balansa 2259*) and *C. angustifolia* Sessé & Moc. ex DC. (*Hassler 11707*).

Dependence on foliar characters in many genera is hazardous, and it has already been noted that this is particularly true in *Cedrela. C. rotunda* Blake was described from *Rose, Standley & Russell 13907,* in which a specimen at U. S. National Herbarium and one at Gray Herbarium have abnormally rounded, nearly circular leaflets. Another specimen at U. S. National Herbarium and the sheet at New York Botanical Garden, probably collected from the same tree, have foliage which is indistinguishable from the bulk of the foliage on specimens of *C. angustifolia* from Mexico. This species is now placed in synonymy.

Blake described *C. Whitfordii* in 1920 on the basis of *Whitford & Pinzon 7* from the Rio Negro Valley of Colombia. From the crown measurements on the label, it is apparent that this collection was made from a fully mature tree. The foliage on these specimens represents the fully mature size and shape of leaflets of *C. angustifolia* grown in a good location. The flowers on this collection are wholly typical of *C. angustifolia,* with no apparent influence from other *Cedrela* species.

The situation regarding the relegation of *C. ciliolata* Blake to synonymy under *C. angustifolia* was previously discussed (p. 323).

In 1922 A. Ducke proposed *C. Huberi,* based on a botanical garden specimen which came from the Rio Capim, Pará. While the calyx margin is somewhat more deeply lobed than that generally found in collections from Central America, this is a normal variation in Brasilian populations where there has been intermixing of *C. angustifolia* with *C. fissilis.* In other characters the specimen falls well within the limits of variation found in *C. angustifolia.*

Tessmann 3510, collected in Peru, was described as *C. longipetiolulata* by Harms in 1927. The foliage of this specimen is obviously from a vigorously growing shoot in which the rachis and petiolules are longer and the leaflets larger than on most specimens of *C. angustifolia.* The inflorescence and flowers do not exceed the variability to be expected in the species.

Finally, in 1933 Harms described *C. pacayana* on the basis of *Tonduz 445* from Guatemala. While I have neither a specimen nor a photograph of this entity, the ample description provided by Harms leaves no doubt that this species must be brought into the synonymy of *C. angustifolia*.

SPECIMENS SEEN

BERMUDA.—Public Garden, St. Georges, *Brown, Britton & Wortley 1744* (st.), Sept., 1913 (NY, PH).

JAMAICA.—Vicinity of Mandeville, *S. Brown 123* (fl.), Feb., 1910 (NY, PH).

MEXICO.—TAMAULIPAS: Vicinity of Tampico, *Palmer 247* (fr.), March–April, 1910 (F, GH, MO, NY). DURANGO: Tamazula, *Gentry 5358* (fr.), Jan., 1940 (F, MO, NY). SINALOA: Rosarito, *Martinez s.n.* (fr.), Dec., 1939 (F). Villa Unión, *Rose, Standley & Russell 13907* (type coll., *C. rotunda* Blake) (fr.), April, 1910 (GH, NY, US). SAN LUIS POTOSI: Tamazunchale, *Edwards 599* (st.), July, 1937 (F, MO). TEPIC: Near Acoponeta, *Rose, Standley & Russell 14468* (fr.), April 12, 1910 (NY, PH). VERACRUZ: Fortuño, Coatzacoalcos River, *Llewellyn Williams 9350* (fr.), Feb.–June, 1937 (F). COLIMA: Melchor Ocampo, *Conzatti 354* (fl.), July, 1897 (GH). MEXICO: Temascaltepec, *Hinton 3394* (fl.), Feb., 1933 (GH). PUEBLA: *Goff s.n.* (fr.), May, 1901 (US). MICHOACAN: Morelia, *Arsène 3075* (fl.), May 15, 1909 (GH, MO). Rincón, *Arsène 2728* (type coll., *C. ciliolata* Blake) (fr. immature), June, 1909 (MO, NY). GUANAJUATO: *Duges s.n.* (type coll., *C. Dugesii* S. Wats.) (fl.), 1880 (GH, NY). YUCATAN: *Steggerda 8 C.* (fr.), 1937 (F). Chichen Itzá, *Lundell & Lundell 7440* (fl.), June–July, 1938 (A, F). OAXACA: Ubero, *Llewellyn Williams 9350* (fr.), April, 1937 (F).

GUATEMALA.—QUETZALTENANGO: Near Rio Samalá between Zunil and Cantel, *Standley 83956* (fr.), Jan., 1941 (F). SACATEPEQUEZ: Volcan de Fuego, *J. D. Smith 2571* (type coll., *C. imparipinnata* C. DC.) (fr.), March, 1892 (GH). San Juan, *Ruano 1372* (fl.) (F). Cuesta de las Cañas above Antigua, *Standley 58874* (fr.), Dec., 1938 (F). GUATEMALA: *Tonduz 731* (fr. immature), July, 1921 (US). Parque La Aurora, *Salas 466* (fl.), Oct., 1923 (US).

HONDURAS.—MORAZÁN: Zamorano, *Williams & Molina 13437* (st.), Jan., 1948 (F, MO). ATLÁNTIDA: Lancetilla Valley near Tela, *Standley 54819* (st.), Dec., 1927–March, 1928 (F).

EL SALVADOR.—Near San Salvador, *Standley 20589* (fr.), Feb., 1922 (NY, US); *Calderón 1132* (fl.), Aug., 1922 (NY, US). Between Santo Domingo and San Sebastián, *Calderón 1210* (fr. immature), 1922 (NY, US). AHAUCHAPÁN: Salto de Atehuecía, *Standley & Padilla 2848* (fr.), Jan., 1947 (F).

NICARAGUA.—Sierra de Managua, *Garnier s.n.* (fl.), 1930–1940 (F).

COSTA RICA.—Monte Verde, *Stork 1678* (fl.), April, 1928 (F). Palmar Sur de Osa, *Allen 5585* (fl.), Aug., 1950 (F, US).

PANAMA.—CHIRIQUI: Progresso, *Cooper & Slater 252* (fl.), July–Aug., 1927 (F, NY); *Cooper & Slater 305* (fl.), July–Aug., 1927 (F, NY). HERRERA: Ocu, *Allen 4082* (fr.), Jan., 1947 (MO). COCLÉ: Aguadulce, *Pittier 4985* (fr.), Dec., 1911 (US). PANAMA: Curundu, *Harvey 5256* (fr.), March, 1946 (F); *Smith & Smith 3254* (fr.), Dec., 1957 (F, PH, NY). Aluajuela, *Pittier 3729* (fl.), May, 1911 (GH, NY). Punta Paitilla, *Standley 30793* (fr.), Jan., 1924 (US). San José Island,

Johnston 323 (fr.), Oct., 1944 (MO); *Erlanson 303* (fl.), June, 1945 (US). Sotto Caballo, *Smith, Smith & Arauz 3322* (fr.), Dec., 1958 (F, PH). Guayabito, *Smith & Smith 3448* (fr.), Dec., 1958 (F, PH).

COLOMBIA.—Pivijay, *Romero C. 1112* (fl.), April, 1948 (F). BOYACA: Guaguaqui, *Whitford & Pinzon 8* (fl. immature), July, 1917 (GH); *Whitford & Pinzon 7* (type coll., *C. Whitfordii* Blake) (fl.), July, 1917 (GH, NY, US). ANTIOQUIA: Medellin, *Toro 265* (fl.), 1927 (NY); *Duque J. 1841* (fr.) (F). Cocorná, *Romero C. 1471* (fl.), Apr., 1949 (F). VALLE DEL CAUCA: La Laguna, *Cuatrecasas 15570* (fr.), Dec., 1943 (F). Río Calima between Pailón and El Coco, *Cuatrecasas 21261* (fl.), May, 1946 (F). Rio Micay, Noanamito, *Cuatrecasas 14222* (fl.), Feb., 1943 (F).

VENEZUELA.—Between Biscaima and La Victoria, *Fendler 2544* (fr.), 1856–57 (GH). CARABOBO: Valencia, *Pittier 8159*, Oct., 1918 (GH). Ptari-tepui, *Steyermark 60690* (fl.), Nov., 1944 (F, NY). MERIDA: La Mata, *C. E. Smith 3490* (fr.), Jan., 1958 (F, PH, MER); near Ejido, *C. E. Smith 3491* (fr.), Jan., 1958 (F, PH, NY, MER, VEN); near Merida, *C. E. Smith 3492* (fr.), Jan. 10–17, 1958 (F, PH, NY, MER); Tabay, *C. E. Smith 3494* (fr.), Jan. 19, 1958 (F, PH, MER). ARAGUA: Maracay, *Smith & Aristeguieta 3476* (fr.), Jan. 11, 1958 (F, MER, PH, NY, VEN).

BRITISH GUIANA.—Wabuwak, Kanuku Mts., *Forest Dept. WB 377* (fr.), Oct., 1948 (NY).

PERU.—La Merced, *Macbride 5400* (fl.), Aug., 1923 (F). HUÁNUCO: Pozuzo, *Macbride 4663* (fr. immature), June, 1923 (F). SAN MARTIN: Zepelacio, *Klug 3696* (fr.), June, 1934 (F, MO, NY). San Roque, *Llewellyn Williams 7397* (fr.), Jan.–Feb., 1930 (F). Middle Ucayali, Contamana, *Tessmann 3510* (type coll., *C. longipetiolulata* Harms) (fl.) (F, NY).

BRASIL.—No locality, *Riedel 658* (fl.) (LE); *Sello 1420* (photo) (fl.) (F); *Sello 1907* (type coll., *C. paraguariensis* Mart. var. *brachystachya* C. DC.) (fl.) (NY, US); *Glaziou 6102* (type coll., *C. Glaziovii* C. DC.) (fr. & fl.) (F); *Glaziou 11844* (type coll., *C. barbata* C. DC.) (fl.) (MO); *Glaziou s.n.* (fl.) (NY); *Moura 60* (photo) (type coll., *C. Mourae* C. DC.) (fl.) (F); *Tatto 4* (fl.), 1941 (US). AMAZONAS: Humayta near Tres Casas, *Krukoff 6408* (fl. immature), Sept.–Oct., 1934 (A, F, MO, NY); *Ducke 215* (fl.), June, 1936 (F, MO, NY). PARÁ: Upper Cupary River, *Krukoff 1128* (fr.), Sept., 1931 (NY); *Capucho 472* (fr.) (F); introduction from Rio Capim, *Ducke 16797* (type coll., *C. Huberi* Ducke) (fl.), March, 1917 (F [photo], US). Belem, *Silva 317* (st.), Nov., 1949 (US). MATTO GROSSO: Rio Paraguay at Diamantino, *Martius 78* (type coll., *C. paraguariensis* Mart.) (fl.) (F [photo], GH, MO, NY). Source of Jatuaraha River, *Krukoff 1680* (fr. immature), Dec., 1931 (A, F, MO, NY). Near Tabajara, *Krukoff 1369* (fl.), Nov.–Dec., 1931 (MO, NY). RIO DE JANEIRO: Theresopolis, *Glaziou 16735* (type coll., *C. longiflora* C. DC.) (fl.), Jan., 1888 (F [photo], NY, PH [photo]). Nova Fribargo, *Curran 760* (fr.), 1918 (GH). Rio de Janeiro, *Glaziou 15881* (type coll., *C. pachyrhachis* C. DC.) (fl.) (F [photo]). MINAS GERAES: Caldas, *Regnell II 39* (type coll., *C. caldasana* C. DC.) (NY). San Terezinha, *Macedo 1267* (fl.), Oct., 1948 (MO). SÃO PAULO: San Carlos, *Helmreicher 39* (fl.), 1843 (F, NY). São Paulo, *Hoehne 28322* (fr.) (NY). Campinas, *Vargas 2326* (fl.), Oct., 1938 (NY); *Santoro 1011* (fl.), Oct., 1937 (US). SANTA CATARINA: Mata da Azambuja, *Seccao de ecologia 115* (fl.), Dec., 1949 (US). Ibirama, *Groieski 38* (fl.), Nov., 1953 (NY).

BOLIVIA.—LA PAZ: Tuire near Mapiri, *Krukoff 10724* (fr.), Sept., 1939 (F, MO, NY).

PARAGUAY.—Cordillera de Altos, *Fiebrig 257* (fl.), Oct., 1902 and Feb., 1903 (F); *Hassler 11707* (selected as type coll., *C. Balansae* C. DC.; see discussion, p. 324) (fr. immature), April, 1913 (F, MO, NY, US). Sierra de Maracayú, *Hassler 5366* (type coll., *C. paraguariensis* Mart. var. *Hassleri* C. DC. & *C. Hassleri* C. DC.) (fl.) (A, MO, NY). Caaguazú, *Hassler 9008* (fl.), Feb., 1905 (MO, NY); *Hassler 9008a* (fr. immature), March, 1905 (NY). Sierra de Amambay, *Hassler 10650* (fl.), Oct., 1907–08 (MO, NY). Asuncion, *Morong 629* (fl. & fr.), 1888–90 (MO, NY, PH).

ARGENTINA.—SALTA: Tartagal, *Schreiter 3898* (fl.), Feb., 1925 (F). La Quinta, *West 8454* (fr.), Feb., 1937 (MO). Abra Grande, *Venturi 5584* (fr.), Nov., 1927 (A). Montealto, *Rodriguez 1146* (fl.), Nov., 1913 (GH). Urundel, *Rodriguez 1146* (fl.), Oct., 1913 (F). JUJUY: Cahlegua, *Lillo 10798* (fr.), Aug., 1911 (F). El Quemado, *Schreiter 5093* (fl.), Oct., 1925 (F); *Venturi 5089* (fl.), Oct., 1926 (A, NY). TUCUMÁN: Tucumán, *Schreiter 10052* (fr. immature), March, 1935 (F). DEL ALTO: Bealcogna, *Venturi 7079* (fr.), June 4, 1928 (F). BURROYACO: Cerro del Campo, *Venturi 7699* (fl.), Nov., 1928 (MO, NY).

Cedrela Lilloi C. DC. Bull. Soc. Bot. Genève ser. 2, 6: 118. fig. 11. 1914. *C. boliviina* Rusby, Descr. S. Am. Pl. 36. 1920. *C. Steinbachii* Harms, Notizblatt. 11: 381. 1932. Plate 9.

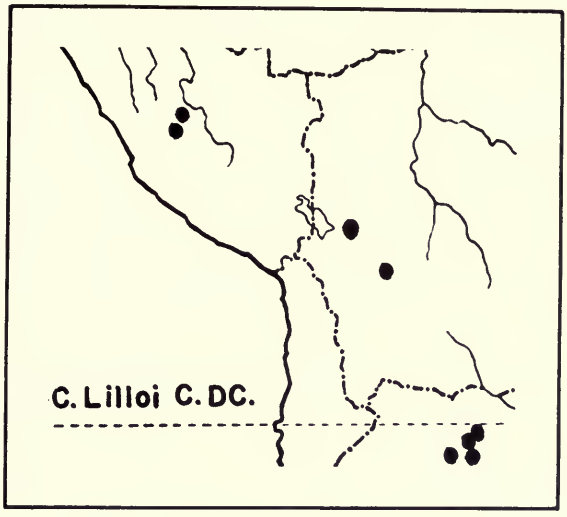
Tree 8 m. to "very tall" (fide *Buchtien 670*). Branchlets glabrous with conspicuous, light-colored lenticels. Leaves variable; leaflets 6 to 9 pairs, 9 to 16.5 cm. long by 2 to 4 cm. wide, ovate-lanceolate, base usually abruptly acute, appearing as though stretched at the top of the petiolule, apex long acuminate to attenuate, acute; glabrous to scattered pubescent beneath; secondary venation close together and very regular. Inflorescence often as long as the leaves, flowers usually crowded, scattered puberulent, bracts deltoid, occasionally subpersistent. Flowers 6 to 10 mm. long; calyx deeply 5-lobed, the lobes subacute to rounded with a light-colored margin, scattered puberulent or pubescent; petals elliptical to subobovate, thickened at the center, puberulent without; filaments broad at point of adnation to gynophore, reduced abruptly above, then sometimes widening again before gradually narrowing upward to the connective; connective fleshy, continued into a conspicuous apiculum; anthers 0.9 to 2.0 mm. long; ovary ovoid, generally glabrous; style usually thick and distinctly angled, 1.2 to 3.0 mm. long, glabrous; capitate stigma 0.5 to 1.0 mm. thick. Fruit to 4.5 cm. long, valves about 2 mm. thick, wings of the central column heavy, extending to the base of the broadened apex, the apex clearly marked where the margins of the valves were adherent.

Trees of hill slopes from 800 to 2800 m. elevation in Peru, Bolivia and Argentina.

Cedrela Lilloi C. DC. was not described until 1914. Most of the collections of this species which I have seen have been made since 1900 and I suspect that the trees either grow in areas not easily accessible or that they are relatively uncommon throughout the range of the species.

The general characters of the flowers point to the close relationship of this species with *C. montana* Turcz. but the foliage is so con-

sistently similar in individual specimens of *C. Lilloi*, and so different from specimens of *C. montana* in texture and leaflet base, that they must remain apart.



MAP 3. Distribution of *Cedrela Lilloi*.

In 1920, Rusby published *C. boliviina* on the basis of *Buchtien 3199*. In 1932, Harms described *C. Steinbachii* on the basis of *Steinbach 8663*. In neither case is there sufficient variation from the type collection of *C. Lilloi* to warrant the maintenance of a separate species.

SPECIMENS SEEN

PERU.—*Rodriguez* (*Ruiz & Pavon*) *s.n.* (st.) (F); *Dombey s.n.* (fl.) (F). Curahuase, *Vargas 1267* (fl.), Nov., 1938 (F, GH). CUZCO: Calca, *Vargas 2942* (fl.), Aug., 1941 (MO).

BOLIVIA.—LA PAZ: Cotaña, *Buchtien 3199* (type coll., *C. boliviina* Rusby) (fl.), Nov., 1911 (NY, US); *Buchtien 670* (fl.), Nov., 1911 (F, MO, NY). COCHABAMBA: Pocona, *Steinbach 8663* (type coll., *C. Steinbachii* Harms) (fl.), Nov., 1928 (F, GH, NY, PH).

ARGENTINA.—TUCUMÁN: Tucumán, *Lillo 11034* (type coll., *C. Lilloi* C. DC.) (fl.), Dec., 1911 (F); *Schreiter 9873* (fl.), Dec., 1934 (F). Famailla, *Schreiter 10454* (fl.), Jan., 1938 (F). BURRUYACU: La Posta, *Venturi 2332* (fl. & fr.), Dec., 1923 (F, MO, NY). Cerro del Campo, *Bailetti 138* (fl.), Jan., 1918 (F). Escaba, *Monetti 1696* (fl.), Dec., 1913 (F). ANDALGALÁ: El Saladillo, *Jorgensen 33* (fl.), Dec., 1916 (F, MO, US).

Cedrela oaxacensis C. DC. & Rose, Contr. U. S. Nat. Herb. 5: 190. 1899. *C. montana* var. *mexicana* C. DC. Mon. Phan. 1: 741.

1878. *C. saxatilis* Rose, Contr. U. S. Nat. Herb. 8: 314. 1905. *C. Tonduzii* C. DC. Bull. Herb. Boiss. ser. 2, 5: 427. 1905. *C. discolor* Blake, Proc. Biol. Soc. Wash. 33: 108. 1920. *C. salvadorensis* Standl. Field Mus. Bot. 4: 215. 1929. *C. poblensis* Miranda, Anal. Inst. Biol. Mexico 13: 453. 1942. Plates 10 and 14.

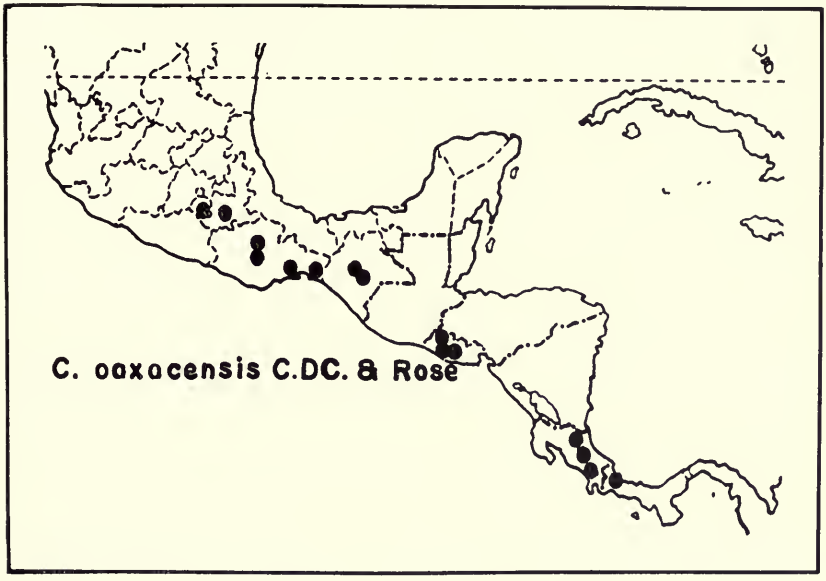
Tree to 40 m. (fide *Little 6077*) but on the rocky hillsides where it is found in Mexico it is often mature at 10 m. Bark deeply fissured and splitting off in long plates. Branchlets often thick, sometimes conspicuously lenticellate. Leaves variable, with 5 to 7 pairs of leaflets 7.5 to 14 cm. long, 2.5 to 6.0 cm. wide, lanceolate to elliptical, base acute to subcordate, subequilateral, apex acuminate obtuse to acute; rarely glabrate, usually veins pubescent above, entire lower surface densely puberulent to pilose. Inflorescence sometimes dense, usually shorter than the leaves, puberulent; bracts subpersistent, to 1.5 mm. long, puberulent. Flowers 5 to 7 mm. long; calyx cup-shaped, shallowly to deeply 5-lobed, occasionally split to the base on one side, 1 to 1.5 mm. deep, generally puberulent; petals elliptical, thickened at the center, puberulent to short pilose without, light at the base shading to rose at the apex along the margins; filaments thick fleshy where they are adnate to the gynophore, narrowing abruptly above; connective wide, ending in a marked apiculum; anthers 1 to 1.8 mm. long; ovary ovoid, glabrous; style usually 2 to 3 mm. long, glabrous; capitate stigma usually about 0.75 mm. thick. Fruit 3.5 to 9 cm. long, valves heavy, usually at least 2 mm. thick, sometimes as much as 7 mm. thick, outer surface lenticellate, smooth to warty; central column with 5 wings extending to the apex over the broadened end, the scars from seed attachment extending basally about one third the length of the column.

Trees of dry to moist areas at elevations up to 6000 feet. In Mexico now largely restricted to steep rocky hillsides where the trees are difficult to fell. Range from Durango, Mexico, to Chiriqui Province, Panama, and perhaps to Peru (see *C. Weberbaueri* Harms).

C. oaxacensis C. DC. & Rose is one of the less well-collected species of *Cedrela*. It was first recognized as a distinct taxon by Casimir De Candolle, who published the new variety *mexicana* for *C. montana* Turcz., based on *Andrieux 483*, collected near Oaxaca in Mexico. The inclusion of this single specimen as a variety of *C. montana* is not surprising, considering the similarity in foliage and flower characters. However, the varietal name could not be elevated to specific rank because it would become a later homonym of *C. mexicana* Roem.

In 1899, De Candolle and Rose recognized three other collections as belonging here and created the specific name *Cedrela oaxacensis* for the entity. The species differs markedly from *C. odorata* and *C. angustifolia* from the same area in its well-developed 5-lobed calyx, whose margin is usually conspicuously lighter in color, in the thickening of the center of the petals, in the sudden reduction in filament width above the point of adnation to the gynophore, and in the very regular secondary venation of the leaflets. Frequently, too, the foli-

age is markedly pilose, but the hairs may be reduced in length and persist only as a dense pubescence on the lower leaf surface. Often the floral bracts are partially persistent rather than early caducous



MAP 4. Distribution of *Cedrela oaxacensis.*

as in the other species. In many ways, though, *C. oaxacensis* is as widely variable as the other *Cedrela* species in the area. From the collections of *C. oaxacensis* cited with the original description, I select *Pringle 4802* as the type collection, although the fruits which sometimes are found with this collection are anomalous (NY, PH, US); they appear to be the fruits of *C. odorata* and must have become mixed in before the distribution of this collection was made.

C. saxatilis was described in 1905 by Rose on the basis of two collections from the same small tree near Cuernavaca, Morelos, Mexico. While the abruptly narrowed filaments, the regularly 5-lobed calyx and the regularly veined leaflets indicate that its place is in *C. oaxacensis,* certain aspects of these collections lead to the suspicion that this taxon represents an intermediate between *C. oaxacensis* and *C. angustifolia.* The calyx is shallowly 5-lobed and split on one side in many flowers; the pubescence is scattered on the under surface of the leaflets; the calyx and petals are only sparingly puberulent; there are no persistent bracts in the inflorescence. Throughout the genus,

such intermediate collections are frequent, and while they must be placed within one species or another, their closer affinities may not be so easily decided as they were in this case. A thorough investigation of the genetic background of *Cedrela* is badly needed. Because it is in flower, I select *Pringle 11806* as the lectotype of *C. saxatilis*.

In 1905, Casimir De Candolle described *C. Tonduzii* on the basis of *Tonduz 11945* from El Copey, Costa Rica. Except for larger leaflets, this collection is almost identical with the type collection of *C. oaxacensis*.

Cedrela discolor of Blake (1920), founded on *Palmer 184* from Durango, Mexico, introduces another set of variations which may have derived from *C. odorata*. The foliage of this collection has leaflets lanceolate in outline with an acute base and a glossy upper surface, although the lower surface is densely puberulent. The inflorescence, on the other hand, is dense and the floral characters are almost wholly those of *C. oaxacensis* so that there is no doubt about the relegation of *C. discolor* to synonymy. Variability in the foliage of *Cedrela* is so widespread that it is untenable to base a species solely upon the foliar characters of a single collection.

Cedrela oaxacensis seems to include a set of genetic factors for the development of a large, heavily lignified capsule. Such a specimen (*Calderon 1007*) was the basis for Standley's *C. salvadorensis*, published in 1929. While the foliage has leaflets of the configuration and venation known within *C. oaxacensis* along with a densely pilose under surface, the capsule of this collection was much heavier than any attributed previously to *C. oaxacensis*. From observations made by myself in southern Mexico in 1957, I am sure that this capsule and that of *Reko 4927* are referable only to *C. oaxacensis*, as the flowers from which these fruits develop agree in detail with those of the type.

Finally, in 1942, Miranda published *C. poblensis* on the basis of a collection from Puebla. The leaflets are more rounded than in previous collections of *C. oaxacensis* but the regular venation, the pilosity beneath, the characters of the capsule and the flowers of another collection from the same place show unmistakably that this is a variant to be included in *C. oaxacensis*.

SPECIMENS SEEN

MEXICO.—DURANGO: San Ramón, *Palmer 184* (type coll., *C. discolor* Blake) (fl.), April–May, 1906 (F, GH, MO, NY). MORELOS: Near Cuernavaca, *Pringle 11806* (type coll., *C. saxatilis* Rose) (fl.), Sept., 1903 (US). PUEBLA: Amatillan near Matamoros, *Miranda 2099* (fr.), July, 1942 (F, GH); *Miranda 2511* (fl.),

Dec., 1942 (F, GH). GUERRERO: Achotla, *Reko 4927* (fr.), July, 1926 (US); *Reko 5071* (fl.), Jan., 1927 (US). OAXACA: Monte Alban, *L. C. Smith 79* (fl., fr. probably extraneous), July, 1894 (GH); *Pringle 4802* (type coll., *C. oaxacensis* C. DC. & Rose) (fl., fr. probably extraneous), Aug., 1894 (B, F, MO, NY, PH, US). Near Oaxaca, *Andrieux 483* (type coll., *C. montana* var. *mexicana* C. DC.) (fl.), July (NY [photo and fragments]). Near Tapanatipec, *Smith & Ruiz 3233* (fl. & fr.), Dec., 1957 (F). Gingola near Tehuantepec, *Smith, Ruiz & MacDougall 3229* (fr.), Dec., 1957 (F, PH). CHIAPAS: Rodeo near Siltepec, *Matuda 4558* (fl.), Aug., 1941 (A, MO, NY). San Pedro, *Mell 623* (fl.), Apr., 1930 (F).

GUATEMALA.—STA. ROSA: Teocinte, *Heyde & Lux 4126* (fl.), Jan., 1893 (GH, NY [photo]). CHIMALTENANGO: Quisache, *Standley 62044* (st.), Jan., 1939 (F).

EL SALVADOR.—Lago de Ilopango, *Calderón 2590* (fr.), May, 1930 (F, US); *Calderón 25* (fl. & fr.), Feb., 1937 (F). Near Los Esemiles, *Tucker 1081* (fr.), March, 1942 (NY, PH). Comasagua, *Calderón 1380* (fl.), Dec., 1922 (NY). Near Chalchuapa, *Calderón 1007* (type coll., *C. salvadorensis* Standl.) (fr.) 1922 (F [photo and fragment]).

COSTA RICA.—El Copey, *Stork 1556* (fl.), April, 1928 (F); *Tonduz 11945* (type coll., *C. Tonduzii* C. DC.) (fl.), April, 1898 (F [photo], GH, NY, US). Near La Presa, *Allen 5280* (fl.), May, 1949 (NY). Barba, *Leon 850* (fl.), July, 1941 (F). Zarcero, *A. Smith 4196* (fl.), May, 1937 (F).

PANAMA.—CHIRIQUI: Rio Chiriqui Viejo, *Little 6077* (fl. & fr.), March, 1943 (F, MO, NY, PH). Near Finca Lerida, *Allen 4751* (fr.), July, 1947 (MO).

Cedrela fissilis Vell. Fl. Flum. 72. 1825, tab. 68. 1827. *C. brasiliensis* var. *australis* A. Juss. in St. Hil. Fl. Bras. Merid. 2: 86. 1829. *C. fissilis* var. *glabrior* C. DC. Monog. Phan. 1: 741. 1878. *C. fissilis* var. *macrocarpa* C. DC. Bull. Herb. Boiss. 2: 574. 1894. *C. hirsuta* C. DC. op. cit. ser. 2, 3: 413. 1903. *C. Regnellii* C. DC. Ann. Conserv. Jard. Bot. Genève 10: 174. 1907. *C. brunellioides* Rusby, Bull. N. Y. Bot. Gard. 8: 99. 1912. *C. Balansae* C. DC. pro parte, Bull. Soc. Bot. Genève, ser. 2, 6: 119, fig. 3. 1914. *C. tubiflora* Bertoni, Anal. Cient. Paraguayos, ser. 2, no. 2: 135. 1918. *C. tubiflora* var. *grandifolia* Bertoni, op. cit. 137. *C. tubiflora* f. *grandifolia* (Bertoni) Buch. & Falc. Darwiniana 10: 464. 1953. *C. tubiflora* var. *intermedia* Bertoni, Anal. Cient. Paraguayos, ser. 2, no. 2: 137. 1918. *C. tubiflora* subsp. *bertoniensis* Bertoni, loc. cit. *C. tubiflora* f. *angustifolia* Bertoni, loc. cit. *C. tubiflora* var. *lagenaria* Bertoni, op. cit. 138. *C. tubiflora* var. *parvifoliola* Buch. & Falc. Darwiniana 10: 464. 1953. *C. macrocarpa* Ducke, Archiv. Jard. Bot. Rio de Janeiro 3: 189, pl. 22. 1922. *C. alliacea* Ducke, nomen nudum, loc. cit. Plate 11.

Tree to 25 m. (fide *Steinbach 6558*). Branchlets glabrate to tawny pubescent, lenticels inconspicuous. Leaves with 6 to 15 pairs of leaflets 8 to 13.5 cm. long by 2 to 4 cm. wide, broad-lanceolate to ovate-lanceolate, base subacute to subcordate, slightly oblique or equal, apex obtuse to acuminate, obtuse or subacute; pubescent to hirsute along the midrib and, at times, along the venules above, short pubes-

cent to hirsute over the entire surface beneath, occasionally only scattered pilose and barbate in the axils of the secondary veins. Inflorescence usually dense, often shorter than the leaves, glabrous along the main axis and puberulent beginning with the tertiary branches to densely pubescent throughout, bracts deltoid-lanceolate, subpersistent. Flowers 6 to 10 mm. long; calyx cup-shaped, 1.5 to 2.5 mm. deep, shallowly to deeply 5-dentate; if shallowly dentate, may be deeply split on one side, puberulent to hirsute; petals elliptical, densely pubescent, pubescence frequently shorter, lighter in color along the margins; filaments broad along adnation to gynophore, contracted and of uniform diameter above, rarely puberulent; anthers apiculate, 1.2 to 1.8 mm. long; gynophore usually thin and elongate, 3.2 to 5.7 mm. long; ovary generally ovoid, glabrous, occasionally puberulent; style 1.3 to 2.4 mm. long, glabrous, occasionally puberulent; capitate stigma 0.4 to 0.9 mm. thick. Fruit 4.5 to 7 cm. long, valves more than 3 mm. thick, heavily lenticellate, central column with the wings extending to the apex.

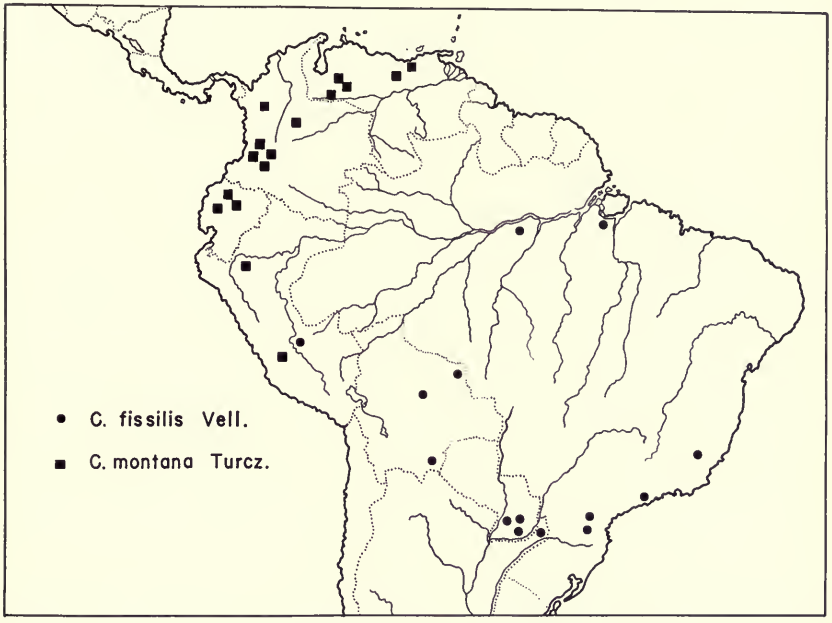
Trees of slopes at elevations of 100 to 300 m. in southern South America.

Cedrela fissilis Vell. is a species which has long been confused with other entities. Because it was one of the earliest described species, many workers seized upon it as a convenient repository, and specimens collected throughout the American tropics were referred here. To be sure, Vellozo's description is very inadequate, but his plate 68 leaves no doubt about the true identity of *C. fissilis*. The pubescence on the branchlet, the back of the leaflets and the branches of the inflorescence is significant; the best confirmation of identity is in the evenly dentate, puberulent calyx and in the thick-valved fruit with the wings of the column continued up onto the apex. The plate stands as a type for the species as Vellozo cited no specimen although he discusses the dimensions of trees he has seen.

Four years later, Adrien de Jussieu published var. *australis* for his new species *C. brasiliensis* in St. Hilaire's *Flora*. Although I have not had an opportunity to examine the material cited "prope Monte-Video-ex herbar. Kunth" Jussieu notes in the explanation for plate 101 "figurae e var. B. sumptae." The description amply differentiates the variety from the species and coincides with the characters of *C. fissilis*. An examination of the detailed drawings on the plate leaves no doubt when one notes the long thin gynophore, the filaments—broad where they are adnate to the gynophore and contracted above—and the conspicuously apiculate anthers. *C. brasiliensis* var. *australis* is placed in synonymy with *C. fissilis*.

Casimir De Candolle described *C. fissilis* var. *glabrior* in 1878. He noted that it is questionably equal to *C. brasiliensis* var. *australis* A. Juss. in St. Hil. Inspection of *Sello 1908* (lectotype collection of *C. fissilis* var. *glabrior*) bears this out and it now goes into synonymy.

Again, in 1894, De Candolle erected var. *macrocarpa* for *C. fissilis* on the basis of *Balansa 2560*. While I have not seen the type collection, De Candolle published an additional note on this variety in 1914, citing *Hassler 12306* and *Hassler 12277*. There is no doubt about the identity of these specimens; for this reason I am placing *C. fissilis* var. *macrocarpa* in the synonymy of *C. fissilis*.



MAP 5. Distribution of *Cedrela fissilis* and *C. montana*.

Cedrela hirsuta C. DC. was published in 1903. An examination of the type collection, *Hassler 4738*, shows this to be merely a more pubescent variant of *C. fissilis*.

Cedrela Regnellii, proposed by C. De Candolle in 1907, is again a variant of *C. fissilis* which can in no way be adequately separated from the other herbarium material which I have examined. I have been unable to see this species in the field, but I have no doubt that the variation of *C. fissilis* follows the same general pattern as that in populations of *C. odorata* and *C. angustifolia*.

C. brunellioides Rusby is a classic example of mixed herbarium material. The resemblance of the foliage to *Brunellia* of the Brunelliaceae is evident; the opposite compound leaves with their obscurely

serrate-margined leaflets probably belong to that genus. They can in no way be forced into the leaf pattern known for American species of *Cedrela* but the fragments of fruit are a *Cedrela* capsule whose thick valves place it in *C. fissilis*.

De Candolle's *C. Balansae* (1914) is a mixed concept. *Hassler 11707*, cited by Buchinger and Falcone as the type collection, obviously belongs elsewhere (see *C. angustifolia* Sessé & Moc. ex DC.). *Balansa 2259* is not before me, but the illustration (fig. 3, p. 120, Bull. Soc. Bot. Genève ser. 2, vol. 6) obviously must have been drawn from this specimen. The drawing agrees in no part with the Hassler collection. The pubescent, evenly 5-dentate calyx, the long, thin gynophore and the pubescent leaf rachis and leaflet of the drawing can be placed nowhere except in *C. fissilis* Vell.

I am adding *C. tubiflora* Bertoni and its numerous varieties, forms and subspecies to the synonymy of *C. fissilis*, although I have not been able to find authentic material. Dra. Maria Buchinger informs me that the Bertoni herbarium specimens are not now accessible and the original specimens could not be located when she visited Paraguay. This material seems to be equatable with *C. fissilis* var. *macrocarpa* C. DC. (Buchinger and Falcone, 1957), and thus comes into the synonymy of *C. fissilis*.

Unfortunately, I have not seen *Ducke 16501* which I am designating lectotype of *C. macrocarpa* Ducke, but a photograph of the type collection clearly shows the true affinities of this species. In addition, I have examined two sheets (*Jard. Bot. Rio de Janeiro 20523*), labeled *C. macrocarpa* by Ducke, which clearly duplicate the type description. The characteristics of the flowers and foliage fit well within the variations noted for *C. fissilis* Vell.

SPECIMENS SEEN

PERU.—Convencion, *Vargas 2141* (fl.), Aug., 1941 (NY). LORETO: Fortaleza, *Llewellyn Williams 4211* (fr.), Oct., 1928 (F). SAN MARTÍN: Zepelacio near Moyobamba, *Klug 3677* (fl.), June, 1934 (A, F, MO, NY, US).

BRASIL.—*Sello 1908* (lectotype coll., *C. fissilis* var. *glabrior* C. DC.) (fl.) (NY); *Sello 1909* (st.) (NY). Villa Boa, *Pohl 2493* (st.) (NY). MINAS GERAES: Sta. Terezinha, *Macedo 724* (fl.), Sept., 1945 (MO). Bello Horizonte, Jard. Bot. *Sampere 7486* (fr.), March, 1934 (F); *Barreto 2001* (fl.), Oct., 1935 (F); *Barreto 7767* (fr. immature), Dec., 1935 (F). Caldas, *Regnell III 361* (type coll., *C. Regnellii* C. DC.) (fl.), Oct. 6, 1857 (S). PARANA: Vallinhas, *Dusén 10788* (fr.), Nov., 1910 (NY); Carambahy, *Dusén 11303* (fl. past anthesis), Dec., 1910 (F, NY); Roca Nova, *Dusén 8666* (fl.), Dec., 1909 (GH, MO, NY). SÃO PAULO: São Paulo, Jard. Bot. *Hoehne 28322* (fl.), Nov., 1931 (NY). Campinas, *Mosén 3829* (fr.), June 20, 1875 (S). PARÁ: Montealegre, *Ducke 16501* (fl. & fr.), Sept., 1916 (F [photo]). Serra

de Santarem, Ducke, *Herb. Jard. Bot. Rio de Jan. 20523* (fl. past anthesis & fr. immature), Jan., 1933 (US).

BOLIVIA.—STA. CRUZ: Between Piray and Tapacani, *Steinbach 2934* (fl.), Oct., 1916 (F). Buenavista, *Steinbach 6558* (fl.), Oct., 1924 (F, MO, NY, PH). Sta. Barbara, *R. S. Williams 1558* (type coll., *C. brunnellioides* Rusby; capsule only, leaves not applicable) (fr.), Aug., 1902 (NY).

PARAGUAY.—Villarica, *Jorgensen 3683* (fl.), 1928 (F, MO, NY, PH). Cordillera de Altos, *Hassler 12277* (fl.), Sept., 1913 (MO, NY). Ypacaray, *Hassler 12306* (fl.), Oct., 1913 (A, MO, NY). Sierra de Amambay, *Hassler 10610* (fl.), 1907–08 (MO, NY); *Hassler 1115* (fl.), 1885–95 (NY); *Hassler 4738* (type coll., *C. hirsuta* C. DC.) (fl.) (F [photo]), MO, NY).

ARGENTINA.—MISIONES: Iguazú, no collector, *4580* (fl.), Sept., 1910 (F); *Curran 671* (fr.), July, 1914 (F, NY).

Cedrela montana Turczaninov, Bull. Soc. Nat. Moscow 31, pt. 1: 415. 1858. *C. bogotensis* Tr. & Planch. Ann. Sci. Nat. Bot. 15: 377. 1872. *C. Rosei* Blake, Proc. Biol. Soc. Wash. 33: 108. 1920. *C. subandina* Cuatrecasas, Fieldiana, Bot. 27: 67. 1950. Plates 12, 13, and 14.

Trees to 50 m. tall (fide *Delgado 208*). Branchlets glabrous, conspicuously lenticellate. Leaves with 6 to 10 pairs of leaflets, 8.5 to 20 cm. long by 3 to 7 cm. wide, base cordate to rounded, occasionally subacute, usually equilateral; apex acuminate, obtuse, rarely attenuate; glabrous or puberulent along the veins above, glabrous to puberulent along the veins beneath, rarely barbate in the axils of the secondary veins or hirsute along the veins beneath. Inflorescences open to dense, about as long as the leaves, puberulent and usually very rough; bracts subpersistent, lanceolate, puberulent, 1 to 2 mm. long; calyx 1.9 to 2.5 mm. deep, regularly and deeply 5-lobed, the margins generally thin and lightly colored in contrast to the general dark color of the calyx, puberulent to pubescent; petals elliptical, thick, densely puberulent without, generally short puberulent within; filaments fleshy along the gynophore, often tapering gradually upward, occasionally abruptly contracted above the point of adnation; anthers prominently apiculate, 1.1 to 2.0 mm. long; connective usually broad and fleshy; ovary hemispherical to ovoid, broadly ribbed, style thick and often angled; capitate stigma 0.4 to 1.1 mm. thick. Fruit 4 to 7 cm. long, smooth and lenticellate without, valves to 1.5 mm. thick, central column with 5 prominent wings extending to the apex, wings often diagonally marked where seeds have pressed against them.

Trees of montane forests at elevations from 1200 to 3100 meters in Venezuela, Colombia and Ecuador.

Cedrela montana Turcz., based on *Moritz 1680* from Colonia Tovar, Venezuela, is a distinct species in the highland area of northwestern South America. The even secondary venation is similar to that of the southern species *C. Lilloi* and *C. fissilis*, but it lacks the former's sudden contraction at the leaf-base and the latter's generally heavy pubescence. The 5-lobed calyx and the stamen form are similar to *C. oaxacensis* in Central America and *C. Lilloi*, but the capsule has

thinner valves with a smooth outer surface, although the wings on the central column extend well up to the apex.

A comparison of a photograph of the type collection of *C. bogotensis* Tr. and Planch. with *Moritz 1680* shows no valid difference between these specimens. While the inflorescence is more open in the latter collection, the significant details of the flowers and foliage are the same. Many collections of this species of *Cedrela* show such wide variation in the length of inflorescence branches and pedicels that this cannot be interpreted as a constant character. Turczaninov's description for *C. montana* is very brief but it agrees with that of Triana and Planchon.

C. Rosei Blake from the vicinity of Quito, Ecuador (*Rose & Rose, 23571*), was distinguished from *C. bogotensis* primarily on the basis of size and pubescence, neither of which is particularly reliable in *Cedrela*. Such features as the shape and venation of the leaflets and the details of the flower are more to be trusted. In these details, *C. Rosei* is indistinguishable from the bulk of the collections which I refer to *C. montana* and I place it in the synonymy of this species without qualification.

Finally, in 1950, Cuatrecasas published *C. subandina* for his collection *21956*. The type specimen, in flower and fruit, cannot be separated from the bulk of material of *C. montana*.

Among the collections cited for *C. montana* are two in which the leaflet form is more nearly that of *C. Lilloi*, being lanceolate with an elongated apex. This is most accentuated in *Cuatrecasas 22017*, which the collector identified as *C. Herrerae* Harms. Floral details leave no doubt as to its proper place nor are the leaflets abruptly acute at the base as they are in *C. Lilloi*. *Macbride 3438*, in young fruit, is a less extreme example of the same leaflet variation which may also be seen in material from Paramo de la Negra in Venezuela.

SPECIMENS SEEN

COLOMBIA.—CUNDINAMARCA: Bogotá, *Dawe 158* (fl.), April, 1916 (US); *Lehmann 7572* (fl.) (F); *Triana 3368* (type coll., *C. bogotensis* Tr. & Planch.) (fl.), 1851–57 (photos, F, PH). VALLE DEL CAUCA; Loma de Barragán, *Cuatrecasas 20898* (fr. immature), April, 1946 (F). Quebrada de los Osos, *Cuatrecasas 20954* (fr.), April, 1946 (F). Quebradahonda, *Cuatrecasas 18407* (st.), Oct., 1944 (F). Rio Pichindé entre Los Cárpatos y El Olivo, *Cuatrecasas 21956* (type coll., *C. subandina* Cuatr.) (fl. & fr.), Aug., 1946. Los Carpatos, *Cuatrecasas 22017* (fl. & fr.), Sept., 1946 (F). La Laguna, *Cuatrecasas 15698* (st.), Dec., 1943 (F). ANTIOQUIA: Medellín, *Duque 1841* (fr.) (NY).

VENEZUELA.—MERIDA: Above Tabay, *Steyermark 56605* (fl.), May, 1944 (F, NY). Morro Aricagua, *Bernardi 6210* (fl.), Feb., 1957 (NY). TACHIRA:

Paramo de la Negra, *Smith & Jorgensen 3545* (fl.), Jan., 1958 (PH); *Aristeguieta 2564* (fl. & fr.), Sept., 1956 (NY); *Bernardi 1167* (fr.), Feb., 1954 (NY). DISTRITO FEDERÂL: Colonia Tovar, *Fendler 140* (fl.), 1854–5 (F [photo], GH, MO); *Moritz 1680* (type coll., *C. montana* Turcz.) (fl.), Dec., Jan. (B, PH [photo]). Avila, *Delgado 208* (fr.), Dec., 1938 (F); *Delgado 300* (fr.), 1940 (US); *Smith & Aristeguieta 3470* (fr.), Jan., 1958 (F, PH); *Smith & Aristeguieta 3471* (st.), Jan., 1958 (F, PH).

ECUADOR.—Cotallas, *Mille s.n.* (fr. & fl.), Dec., 1923 (MO, NY, PH). Quito, *Rose & Rose 23571* (type coll., *C. Rosei* Blake) (fl.), Nov., 1918 (GH, NY). Valle de Tablas, *Acosta 6031* (st.), Oct., 1943 (F).

PERU.—Cani, *Macbride 3438* (fr. immature), April, 1923 (F).

Cedrela Weberbaueri Harms in Macbr. Field Mus. Bot. 8: 82. 1930.

Small tree to 10 m. (fide *Macbride 3800*). Leaves with 4 pairs of leaflets 7 to 17 cm. long by 4 to 10 cm. wide. Leaflets ovate to elliptical, either densely pilose on both surfaces or scattered pilose above, more densely pilose beneath; base rounded, apex short acuminate. Fruiting inflorescence puberulent. Fruit to 5 cm. long; valves thin (1.0 mm.); column with the wings extending nearly to the apex.

This species, based on only two Peruvian collections from the eastern Andean foothills, does not belong with the other South American species. The Macbride collection, which is perhaps the more representative, is so close to *C. oaxacensis* that I can almost predict the floral characters. Had similar material been found west of the Andes I would have placed it with the Central American species. In view of the disjunction in range and the mountain barrier, it is best to leave it as a little-known species endemic to Peru. Perhaps future collections will show that *C. oaxacensis* does indeed have a southward extension along the Andes and the Macbride collection can then be included. The sterile Weberbauer collection may not belong in the genus; without flowers or fruit this is but a guess.

SPECIMENS SEEN

PERU.—HUÁNUCO: Yanano, *Macbride 3800* (lectotype coll., *C. Weberbaueri* Harms in Macbr.) (fr.), May, 1923 (F). HUANCAVELICA: Near San Georgio, *Weberbauer 6568* (st.), 1909–1914 (F, GH).

Species Excluded

Cedrela alternifolia (Mill.) Steud. Nomenclator Botanicus enumerans, ... 1821.

Cedrus alternifolius Miller, Gard. Dict. (ed. 7). 1759. Described as "folius alternis simplicibus . . . ." with a five-cornered pointed fruit. This was excluded from *Cedrela* by A. de Jussieu (1830) and properly so, as all of the American species now known have pinnate foliage and smoothly ovoid capsules.

Literature Cited

ACOSTA SOLIS, M.
1939. Principal timbers used in the Sierra del Ecuador. Trop. Woods 57: 2–3.

ADANSON, M.
1763. Familles des plantes, 2: 343.

ARNOLD, C. A.
1936. The occurrence of *Cedrela* in the Miocene of western America. Am. Midl. Nat. 17: 1018–1021.

BASCOPÉ, F., *et al.*
1957. El genero *Cedrela* en America. Fac. Cienc. For. Desc. de Arboles 2.

BERRY, E. W.
1916. The lower Eocene floras of southeastern North America. U. S. D. I., Geol. Surv. Prof. Pap. 91: 253–255.
1930. Revision of the lower Eocene Wilcox flora of the southeastern United States. U. S. D. I., Geol. Surv. Prof. Pap. 156: 95.

BOL. DIR. GEN. FOR. Y CAJA (Mexico). 3 (1942) and 5 (1944).

BROWN, ROLAND
1937. Further additions to some fossil floras of the western United States. Journ. Wash. Acad. Sci. 27: 506–517.
1940. *In* LOUGHLIN, G. F., Shorter contributions to general geology. U. S. D. I., Geol. Surv. Prof. Pap. 186: 178–179.

BROWN, ROBERT
1814. General remarks, . . . p. 64. (Acc. to De Candolle, Prodromus).

BROWNE, PATRICK
1756. Civil and natural history of Jamaica, p. 158, pl. 10.

BUCHINGER, M., and FALCONE, R.
1957. Las meliaceas argentinas. Rev. Invest. For. 1: 9–58.

CHANEY, R. W.
1927. Geology and paleontology of Crooked River Basin with special reference to the Bridge Creek flora. Carn. Inst. Wash. Publ. 346 (4): 125–126.

DE CANDOLLE, CASIMIR
1878. Monographiae Phanerogamarum 1: 399–752.
1908. A revision of the Indo-Malayan species of *Cedrela*. Rec. Bot. Surv. Ind. 3 (4): 357–376.

DE CANDOLLE, PYRAMUS
1824. Prodromus systematis naturalis, ... 1: 619–626.

ERDTMAN, G.
1952. Pollen morphology and plant taxonomy. Angiosperms.

HARMS, H.
1896. Meliaceae in die naturl. Pflanzenfam. 3 (4): 258–308.
1940. Meliaceae in die naturl. Pflanzenfam. (ed. 2), 19 (bl.): 1–172.

INTERNATIONAL CODE OF BOTANICAL NOMENCLATURE, 1956.

JUSSIEU, A. L. DE
1789. Genera plantarum, ... pp. 263–266.

JUSSIEU, ADRIEN DE
1830. Mémoire sur le groupe des Méliacées. Mem. Mus. Hist. Nat. 19: 153–304.

JUSSIEU, BERNARD DE
1759. Cat. Hort. Trianon.

KRIBS, D. A.
1930. Comparative anatomy of the woods of the Meliaceae. Am. Journ. Bot. 17: 724–738.

KUNTZE, O.
1891. Revisio generum plantarum, ... 1: 108–111.

LAMPRECHT, H.
1956. El cedro. Bol. Fac. Cienc. For. 11 (inside covers).
(?) Estudios sobre la capacidad germinativa de las semillas de *Cedrela odorata* L. en relacion con el metodo de almacenamiento. Rev. Fac. Cienc. For. 12: 3–24.

LINNAEUS, C.
1759. Systema naturae (ed. 10), 2: 940.

METCALFE, C. R., and CHALK, L.
1950. Anatomy of the dicotyledons 1: 349–358.

MILLER, PHILLIP
1759. The gardner's dictionary . . . . (ed. 7).

RECORD, S. J.
1941. American timbers of the mahogany family. Trop. Woods 66: 7–33.

RECORD, S. J., and HESS, R. W.
1943. Timbers of the New World, 363–365.

ROEMER, M. J.
1846. Familiarum naturalium regni vegetabilis synopsis monographicae . . . . 1, Hesper. 137.

SIMMONDS, N. W.
1954. Chromosome behavior in some tropical plants. Heredity 8: 139.

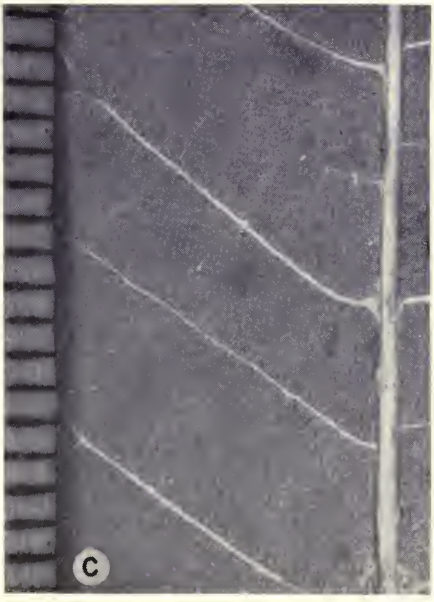
SMITH, EARL E.
1954. The forests of Cuba. Maria Moors Cabot Found. Publ. 2.

VEILLON, J. P.
1955. Geografia, composición, importancia y costo de las explotaciones maderas en el estado Barinas, Venezuela. Bol. Fac. Cienc. For. 9: 71–124.

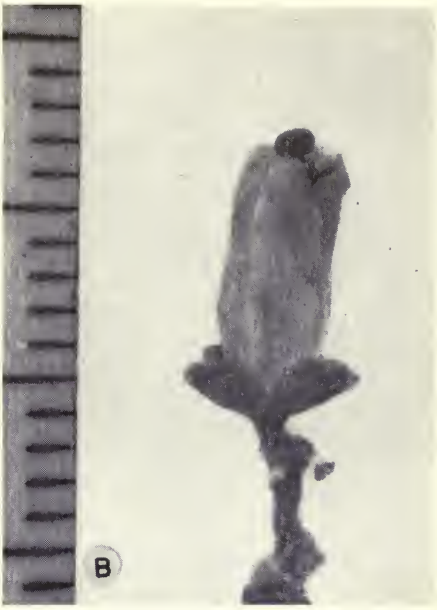
VILLAÇA, HELENA, and FERRI, M. G.
1954. On the morphology of the stomata of *Eucalyptus tereticornis*, *Ouratea spectabilis* and *Cedrela fissilis*. Univ. de São Paulo, Fac. Fil., Cienc., e Let. Bol. 173: 33–51.

WILSON, P.
1924. Meliaceae, in North American Flora 25: 263–296.

PLATES



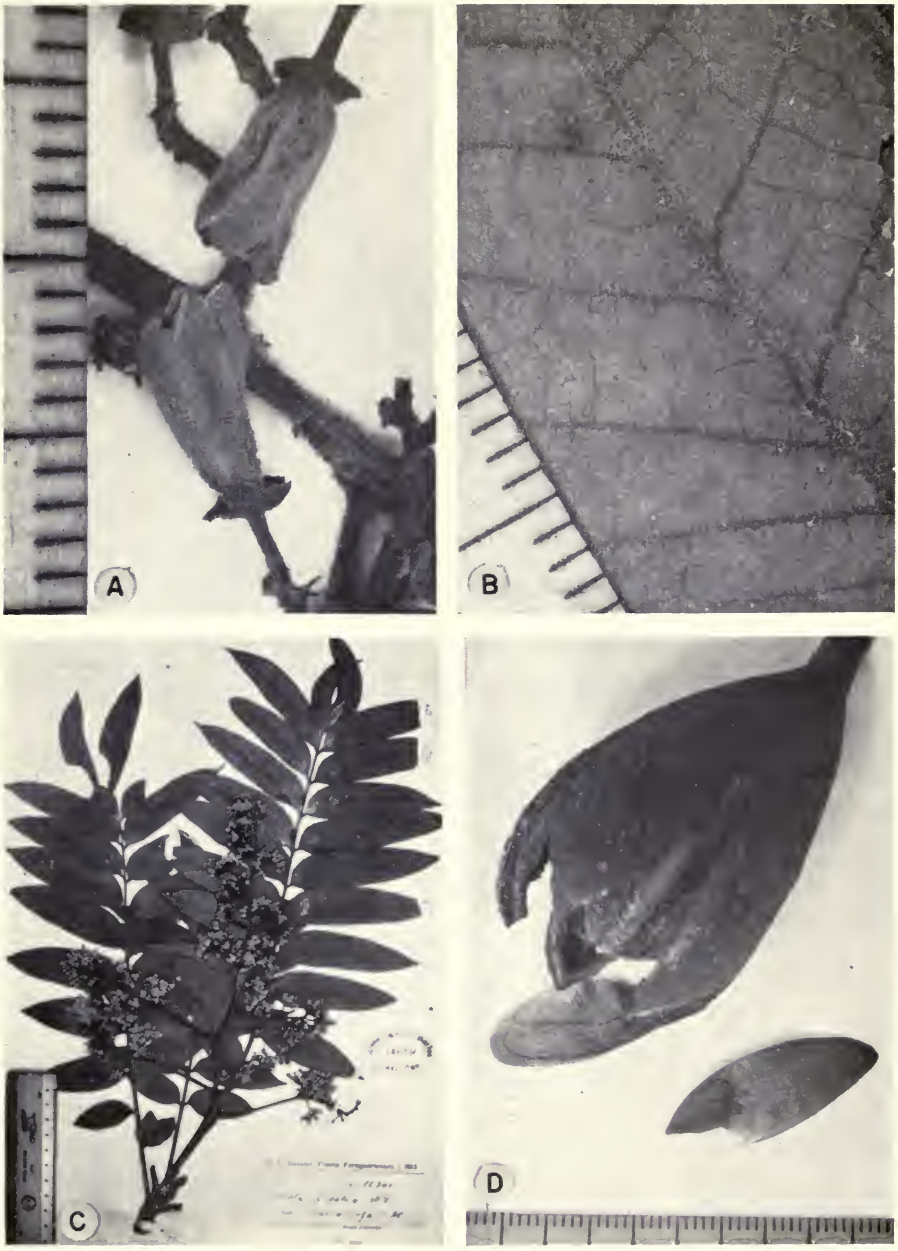
Cedrela odorata L. A, Representative specimen. B, Floral detail. C, Under surface of leaf; dark venules are frequent in this species. D, Fruit showing broad apical area on column.



Cedrela angustifolia Sessé & Moc. ex DC. A, Representative specimen. B, Floral detail. C, Under surface of leaf with puberulent veins. D, Fruit showing small apical area on column.

Cedrela Lilloi C. DC. A, Representative specimen (type collection). B, Fruit; note that wings extend to column apex. C, Under surface of leaf with acutely protracted base. D, Floral detail.

Cedrela oaxacensis C. DC. & Rose. A, Representative specimen. B, Floral detail. C, Fruit; note large size. D, Under surface of leaf showing pubescence.



Cedrela fissilis Vell. A, Floral detail. B, Under surface of leaf showing pubescence. C, Representative specimen. D, Fruit; note valve thickness.

Cedrela montana Turcz. A, Representative specimen. B, Floral detail. C, Under surface of leaf. This collection is barbate in the axils of the secondary veins. D, Fruit.

EXPLANATION OF PLATE 13

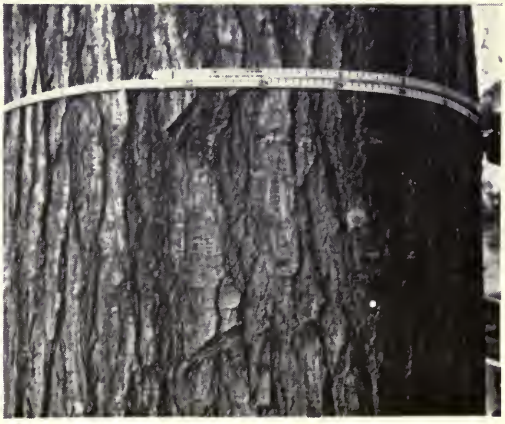
Upper left: *C. montana* Turcz. on Avila near Caracas, Venezuela.

Upper right: Bark detail of *C. montana*.

Middle right: Seedlings of *C. odorata* L. in forestry nursery near Maracay, Venezuela.

Lower left: *C. angustifolia* Sessé & Moc. ex DC. along road near La Victoria, Venezuela.

Lower right: Bark detail of *C. angustifolia*.



EXPLANATION OF PLATE 14

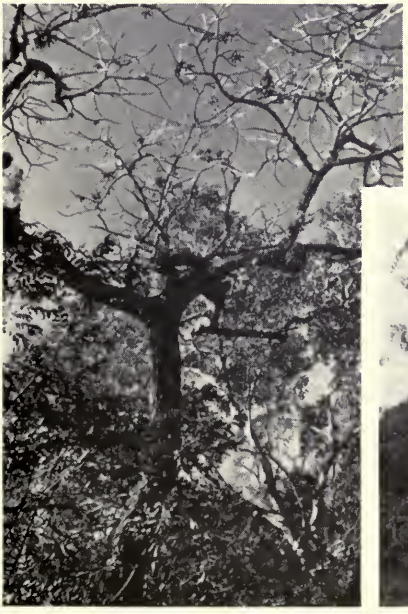
Upper left: Mature tree of *C. montana* in forest at La Mucuy near Merida, Venezuela (estimated height, 125 feet).

Upper right: Fruiting branches of *C. angustifolia* in parkway planting at Maracay, Venezuela.

Center right: Partially finished cabinet of *cedro rojo* (probably *C. odorata*) in cabinet-maker's shop at Tehuantepec, Mexico.

Lower left: *Cedrela oaxacensis* C. DC. & Rose on hill slope near Tapanatipec, Mexico; probably standing because compression wood in curved trunk makes it unsuitable for use.

Lower right: Seedling stand of *C. angustifolia* near Guayabito, Panama. The variation in these trees is notable even in the characteristics of the bark.



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